Exploration of the taxonomy of some Pleistocene Cervini (Mammalia, Artiodactyla, Cervidae) from Java and Sumatra (Indonesia): a geometric- and linear morphometric approach

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Abstract:

Third molars of extant- and fossil Southeast Asian deer were metrically compared using a linear- and geometric morphometric approach and discussed in relation to known taxonomic information from the literature. Our analysis suggests the presence of medium sized deer of the genus Axis and large sized taxa of the genus Cervus s. l. in Java. Axis lydekkeri and A. javanicus are considered valid taxa, with A. lydekkeri probably related to the subgenus Hyelaphus. The large deer, such as Cervus kendengensis, C. stehlini and C. problematicus are most likely of the subgenus Rusa, the former two closely related to extant C. timorensis. The Sumatran fossils are members of the subgenus Rusa, but not necessarily conspecific with extant Cervus (Rusa) unicolor.

Keywords: Cervidae, Cervini, taxonomy, Quaternary, Sundaic subregion, geometric morphometrics

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1. Introduction

Due to the presence of a sizable number of hominin remains (Kaifu *et al*. 2005) and the diverse fauna that has been found in association with them, the Pleistocene paleontological deposits of Java are recognized as some of the richest in Southeast Asia (e.g. Dubois 1907, 1908, Von Koenigswald 1933, 1935). Systematic collection of fossils since the late 19th century eventually led to the description of the *Pithecanthropus erectus* - (now *Homo erectus*) lectotype and resulted in the description of large numbers of mammalian remains from Java and Sumatra (de Vos 2004).

After more than a century the description and taxonomic status of most large mammal groups from this region has been discussed in detail (e.g. von Koenigswald 1933, 1935, Hooijer 1948, 1955, 1958, 1960, 1962, Hardjasasmita 1987). However, this is not the case for Cervidae since the family is morphologically conservative in nature (Lister 1996), complicating the identification and inferred taxonomic status of the often fragmentary remains. Consequently more than a dozen taxa have been described for the Pleistocene of Java over the course of the last century (e.g. Martin 1888, Dubois 1907, Stremme 1911, von Koenigswald 1933, 1934). The validity of some of these species can be questioned.

Geographically this paper is concerned with the Pleistocene deer of Sundaland, which is the name given to the biogeographical region that includes Borneo, Sumatra, Java, Bali, Palawan, the Mentawai Islands and the Malay Peninsula up to the Kra Isthmus (Harisson *et al*. 2006). In the past it also included the landmass in between these islands that emerged during periods of lower sea level (Voris 2000). In practice the emphasis of this work is on Sumatra and especially on Java, as pre-modern mammal fossils are scarce in the other regions of Sundaland.

While the taxonomy and phylogeny of extant deer remains partially unresolved, recent genetic and morphological studies have shed new light on this complex family (Groves & Grubb 1987, Randi *et al*. 1998, Pitra *et al*. 2004, Meijaard & Groves 2004,). Here we synthesize several decades of research to provide an overview of the medium- and large sized fossil cervids described from the Pleistocene deposits of Java and Sumatra. We further explore through morphometric analysis how some of these palaeospecies may be related to extant taxa in the light of recent taxonomic insights. Although the results of our analysis may provide some additional data on extant deer relationships, it is not our intention to give a complete taxonomic revision of the recent Cervidae.

The focus of this paper is on the true antlered deer or the tribe Cervini. Muntjaks (*Muntiacus* spp.) also form part of the Pleistocene faunas of Java and Sumatra (Badoux 1959, Van den Brink 1982, de

54 Vos 1983), but don't pose the same problems in terms of (applied) taxonomy and are not included in
55 this study.
56
57 Cervini are known from large parts of Eurasia, North Africa and America (Meijaard & Groves 2004),
58 but tropical Asia was probably the heartland of deer radiation (Geist 1998). Since the Neogene and
59 especially during the Quaternary much of this radiation was induced by increasing climatic
60 fluctuations. This led to significant changes in Cervid ecology, behavior and morphology over time
61 (Geist 1998).

62 In Southeast Asia, an area of major importance in deer evolution, regional geography and
63 environments are thought to have been heavily influenced by Pleistocene glacio-eustatic sea level
64 fluctuations (Van den Bergh *et al*. 2001). At times of lower sea level, large parts of the Sunda shelf
65 must have been exposed, connecting major islands like Borneo, Sumatra and Java to the Asian
66 mainland (Bird *et al*. 2005, Voris 2000) (fig.1). Undoubtedly these changes must have had an effect
67 on speciation in certain mammal groups (Cranbrook 2010).

68 <Fig. 1>

69 A number of Cervini are currently present in Eurasia (fig. 2). As with most of the other deer tribes,
70 the taxonomy of the Cervini remains controversial (Groves 2007). An overview of the taxonomic
71 scheme followed in this paper is given below.

72 <Fig. 2>

73 In the classic work by Groves and Grubb (1987), the genus *Cervus* (sensu lato) is divided into four
74 subgenera, namely *Rusa* (containing *C. timorensis, C. unicolor, C. alfredi* and *C. mariannus*), *Rucervus*
75 (containing *C. eldii*, *C. duvaucelli* and *C. schomburgki*), *Prezwalskium* (containing only *C. albirostris*)
76 and *Cervus* (sensu stricto) (containing *C. elaphus* and *C. nippon*). The genus *Axis* is composed of the
77 subgenera *Axis* (containing *Axis axis*) and *Hyelaphus* (containing *Axis kuhlii, Axis calamianensis* and

78 *Axis porcinus*) (Meijaard & Groves 2004). The Genus *Dama* is represented by only one species (*Dama*
79 *dama*), while Pere David's deer (*Elaphurus davidianus*) may have been the result of hybridization
80 between two unknown species (Groves & Grubb 1987), most likely from the *Rucervus* and *Cervus*
81 subgenera (Meijaard & Groves 2004).

82 More recent genetic research has shed doubt on some of these relationships. Using mitochondrial
83 DNA sequences Randi *et al.* (2001) argued for a fusion of the subgenera R*ucervus* and *Elaphurus*,
84 while also proposing a revision of the subgenus *Rusa*. Another mitochondrial DNA analysis by Pitra *et*
85 *al*. (2004) proposes several changes on the generic level as well as at the species level. In that study
86 (Pitra et al. 2004) genera are demarcated using a 5 mya time criterion, resulting in the recognition of
87 the genera *Rucervus* (with *R.duvaucelli* and *R. schombrugki*), *Axis* (only containing *Axis axis* and
88 excluding *Hyelaphus*) and *Dama* (with *Dama dama* and *Dama mesopotamica* separated as true
89 species). All other species were placed in *Cervus*, with possibly *Cervus eldii* under its own genus
90 *Panolia* and *Cervus davidianus* under its own genus *Elaphurus* (Pitra *et al.* 2004). In addition *Cervus*
91 *elaphus* was argued to be paraphyletic and *Axis porcinus* more closely related to the *Rusa*-deer than
92 to *Axis axis* (Pitra *et al.* 2004).

93 As these analyses remain sometimes incompatible (see overview table 1), we chose to maintain a
94 relatively conservative view regarding living deer taxonomy based on the scheme by Groves and
95 Grubb (1987), but keeping in mind more recent developments. A summary of the taxonomic scheme
96 used in this paper is given in table 1.

97 <Table 1>

98 **2. The Pleistocene Cervini from Java and Sumatra**

99 Southeast Asian Pleistocene deer are known from the mainland (e.g. Auetrakulvit 2004, Zeitoun *et al*.
100 2005, Bacon *et al*. 2008a, 2008b) as well as from several islands west of Wallace's line (Van den

101 Bergh *et al*. 2001). As far as Sundaland is concerned, deer fossils are found in deposits from Borneo,
102 Sumatra, Java, Peninsular Malaysia and Palawan.

103 The paleontological record of Java is by far the best known in the region (Louys *et al*. 2007). Cervids
104 have been identified in a number of sites. Two of the living Cervini are currently found in Java, *Cervus*
105 *(Rusa) timorensis* and *Axis (Hyelaphus) kuhlii*. Both are known from the paleontological record in
106 addition to a series of extinct taxa, a large number of which have been described by von Koenigswald
107 (1933, 1934). A list of taxa known from the Javanese Pleistocene record and their synonyms is
108 summarized in table 2. Of the extinct species only *Axis javanicus*, *Cervus zwaani*, *Axis lydekkeri* and
109 *Cervus problematicus* are recognized by the International Commission on Zoological Nomenclature
110 (ICZN) (Polaszek *et al*. 2005).

111 The Bawean deer (*Axis kuhlii*), that currently has a distribution limited to Bawean island north of
112 Java, is thought to have been present on the main island of Java at least during the early Holocene, as
113 supported by finds from Wajak cave (Van den Brink 1982). Its relationship with the Pleistocene deer
114 from Java is not well understood.

115 <Table 2>

116 *Cervus* (*Rusa*) *timorensis* is almost certainly present in several Holocene cave deposits such as
117 Sampung cave (Dammerman 1934), Wajak cave (van den Brink 1928) and Hoekgrot (Storm 1990).
118 *Cervus hippelaphus* described at the Middle Pleistocene locality of Ngandong by von Koenigswald
119 (1934) is a junior synonym for *Cervus* (*Rusa*) *timorensis* (Hedges *et al*. 2008) and *Cervus* sp., known
120 from the Late Pleistocene Punung fauna (Badoux 1959, Westaway *et al*. 2007), might also belong to
121 this species. Besides this, a large number of specimens from the various Pleistocene localities of Java
122 have been attributed to the sub-genus *Rusa*, but it is unclear whether they should be included in
123 *Cervus* (*Rusa*) *timorensis* (Zaim *et al*. 2003).

Another extant species mentioned for the Javanese Holocene record is *Cervus* (*Rucervus*) *eldii* (Dammerman 1934). A single incomplete antler from Sampung cave was identified by Dammerman (1934). The author describes the fragment as peculiar due to the fact that the brown tine forms an almost continuous curve with the beam. Similar specimens from the Middle Pleistocene site of Ngandong were however described by von Koenigswald (1933) as a subspecies of *Cervus* (now *Axis*) *javanicus*. No other fragments of *C. eldii* are known from Java.

A smaller species, *Axis lydekkeri*, was described by Martin (1888) on the basis of a single antler. The almost complete antler is smooth, groove-less (Martin 1888) and has a typical lyre-shape (Zaim *et al*. 2003). The type specimen probably belongs to a sub-adult individual (Dubois 1908). This species is relatively well known and identified by several different researchers (Dubois 1908, Vogel von Falckenstein 1910, Stremme 1911, von Koenigswald 1933, 1934). Although Martin (1888) considered its morphology different from any known recent deer, it was Dubois (1891) who noticed its similarity to the Indian *Axis*-deer. Meijaard and Groves (2004) argue that it should probably be classified under the subgenus *Hyelaphus*. *Axis lydekkeri* is abundant in Trinil (von Koenigswald 1934), but also present at several other sites such as Pitu, Watualang (von Koenigswald 1933), Ngandong (von Koenigswald 1934) and Sangiran (Moigne *et al*. 2004a, 2004b). It is thought to be similar in size to *Axis* (*Hyelaphus*) *porcinus* (Zaim *et al*. 2003) and slightly smaller than *Axis* (*Axis*) *axis* (Vogel von Falckenstein 1910).

Axis javanicus, another member of the genus *Axis*, was described by von Koenigswald (1933, 1934). No type specimen was designated, but many antler pieces are known from late Quaternary contexts in eastern Java (Zaim *et al*. 2003). This species is best known from Ngandong (von Koenigswald 1933) in addition to Watualang, Pandejan and possibly Pitu (Zaim *et al*. 2003). The antlers of this species are described as slightly pearled and, unlike *Axis lydekkeri*, with and angle between the beam and brown tine of at least 90° and usually with an accessory tine within this angle (von Koenigswald 1933, Zaim *et al*. 2003). According to Moigne (2004) it is most similar in size to *Axis* (*Hyelaphus*) *kuhlii*, and might be considered a subspecies of this taxon. Meijaard and Groves (2004) on the other hand

consider it synonymous with- or closely related to- a form of the extant chital (*Axis axis*), that migrated from the mainland to Java during the Late Pleistocene.

Cervus zwaani (von Koenigswald 1933) is based on four mandibles and an upper third molar from Bumiaju in Western Java. In addition, von Koenigswald provisionally attributed some fragments from Perning (von Koenigswald in de Terra & Patterson 1939, de Terra 1941), Sangiran and Baringinan (von Koenigswald 1934) to this species. No antlers have been attributed to *Cervus zwaani* (Zaim *et al*. 2003), but von Koenigswald (1933) claimed the species was slightly larger than *Axis lydekkeri* and that the premolars were more robust than in the latter species. According to Zaim *et al*. (2003), this species may however be a junior synonym of *Axis lydekkeri*, because it is morphologically indistinguishable from this species and the supposed larger size is not supported by comparative measurements on *A. lykkeri* fossils in the collections in Leiden (Zaim *et al*. 2003, Bouteaux 2005).

Besides these animals of smaller stature that might be attributed to the genus *Axis*, there are also a series of larger deer known from the Javanese paleontological record. The majority of these have been assigned to the subgenus *Rusa*. Their relationship with the only species of this subgenus living today in Java (*Cervus* (*Rusa*) *timorensis*), remains controversial.

One of these larger taxa is *Cervus stehlini*. This species was described on the basis of several mandibles and a few antler fragments from the Early Pleistocene Bumiaju locality (von Koenigswald 1933). Von Koenigswald (1933) considered it distinct from *Cervus hippelaphus* (now *Cervus* (*Rusa*) *timorensis*), based on the peculiar morphology and slenderness of its premolars. Besides these small differences however, the author noted its similarity in size and shape to the living form (*C. timorensis/C. hippelaphus*) (von Koenigswald 1933).

The largest species recognized in the fossil record of Java is *Cervus* (*Rusa*) *problematicus.* This taxon was described by von Koenigswald (1933) from the Early Pleistocene of Bumiaju on the basis of a partial cranium and a lower first molar. Later von Koenigswald (1934) included other remains in this

173 species and placed it under the subgenus *Rusa*. The skull has recently been re-identified as a bovid
174 and should be excluded from this taxon (van den Bergh pers. comm. in Zaim *et al*. 2003).

175 The taxonomic status of *Cervus* (*Rusa***)** *oppenoorthi* is also debated. This species is known from a
176 number of antler fragments from Pitu and Semboengan and was described as strongly pearled and
177 similar to *Cervus Kuhlii* (now *Axis* (*Hyelaphus*) *kuhlii*), but larger in size (von Koenigswald 1933). Von
178 Koenigswald (1933) considered it distinct from the large Javanese *Rusa* (*Cervus* (*Rusa*) *timorensis*)
179 and from *Axis lydekkeri*. He furthermore concluded that it was probably most closely related to *Axis*
180 (*Hyelaphus*) *kuhlii.* This was later confirmed by van Bemmel (1944), who considered it possibly even a
181 subspecies of *A. kuhlii*. Zaim *et al*. (2003), on the other hand have argued that it was probably more
182 closely related to the *Rusa*-subgenus. It should however be noted, that at the time von Koenigswald
183 classified these specimens, the Bawean deer (now *Axis* (*Hyelaphus*) *kuhlii*), was considered a member
184 of the subgenus *Rusa* (von Koenigswald 1933). Moreover the taxonomic position of *Hyelaphus* is still
185 a matter of controversy and some recent molecular studies support a close relationship between this
186 subgenus and the *Cervus* (*Rusa*) *timorensis/Cervus* (*Rusa*) *unicolor*-clade (Pitra *et al*. 2004).

187 Besides those already mentioned, von Koenigswald (1933) also noted the presence of several forms
188 in the fossil record that he could not assign to a specific taxon. Whether these finds should be
189 considered separate species from the ones mentioned here, is unclear. In Watualang he found a very
190 small but badly preserved antler fragment that he was unable to assign to a species and therefore
191 identified it as *Cervus* sp. Later in the same publication, the author mentions a partial skull with
192 antlers from Sembungan that he does not identify (von Koenigswald 1933). The author noticed its
193 similarity to both *Cervus* (*Rusa*) *unicolor* and to *Cervus* (*Rusa*) *timorensis*. However, due to the
194 unusual morphology of the cranium, notably a sharp kink in the skull profile, it was not included in
195 any of the known species, but cautiously placed under *Cervus* (*Rusa*) sp. (Von Koenigswald 1933).

196 Others also noticed the occurrence of other, larger species in the Javanese deposits. In 1888, Martin
197 mentioned the presence of a larger sized deer (*Cervus* sp.), besides *Axis lydekkeri*, amongst the

198 known Javanese fossils at that time. Dubois (1891) came to the same conclusion, and also
199 acknowledged the existence of at least two different deer amongst the fossils he had collected in the
200 field. Although at the time he did not yet assign these finds (*Cervus* sp.) to a new species, he
201 mentioned that the antlers were much heavier than the ones of *Axis lydekkeri* (Dubois 1891). He
202 made a similar statement in 1907 adding that "…the other, rarer deer species are similar in shape to
203 the large deer living in Java today [*Cervus timorensis*], but also to a certain extent to the Indian
204 Sambar [*Cervus unicolor*]." (Dubois 1907). In the absence of a type specimen, it is unclear what fossil
205 material the author was referring to in these cases. Furthermore other researchers have also
206 provisionally attributed cervid fossils to the subgenus *Rusa* without identifying them to species.
207 These include *Cervus* sp. sensu Stehlin (1925), *Cervus* sp. sensu Stehn & Umgrove (1926) and *Cervus*
208 (*Rusa*) sp. sensu Aziz & de Vos (1999).

209 A new species of large stature that was described by Dubois is *Cervus kendengensis* (Dubois 1908).
210 This form was considered similar to the recent *Cervus hippelaphus* (now *Cervus* (*Rusa*) *timorensis*). It
211 was given specific status mainly due to the shorter and thicker anters (Dubois 1908). Although
212 Dubois (1908) gave only a short description and did not designate any type specimens, a sizable
213 number of the larger Cervidae in the collection of the Naturalis were placed by him under this taxon.

214 In the same publication (Dubois 1908) the author also proposed a new species: *Cervus*
215 *palaeomendjangan*. In his description, Dubois characterizes this second large Cervid by the peculiar
216 morphology of its antlers with typically small tines pointing outwards and to the front, similar to the
217 recent large Javanese deer (*Cervus* (*Rusa*) *timorensis*). This species was not recognized by von
218 Koenigswald (1933).

219 Of special interest in other areas of Sundaland are a number of remains found in cave deposits in the
220 Padang highlands of Sumatra. Based on their biostratigraphic similarity to the Javanese Punung
221 fauna, these sites can probably be dated in the early Last Interglacial (between 128 +/-15 and 118 +/-

3 ka) (de Vos 1983, Westaway *et al*. 2007). Dozens of isolated teeth were found in these caves. Besides Muntjak (*Muntiacus muntjac*) a large deer of the (sub-) genus *Rusa* is present (de Vos 1983).

A number of cave sites in Borneo (Harrison 1998, Piper *et al*. 2008) have provided evidence of cervids, but the Pleistocene record in Borneo does not go back further than about 45,000 years (Niah cave) and contains only extant species like sambar (*Cervus unicolor*) and muntjak (*Muntiacus* sp.) (Cranbrook 2010). The fossil record in peninsular Malaysia is particularly poor. A small collection from Ipoh (Kinta Valley, Perak), thought to be of Middle Pleistocene age, possibly contains a large deer of the (sub-) genus *Rusa* (Hooijer 1962). In some recently collected material of uncertain age (from Perak and Selangot) the presence of *Cervus unicolor* was attested (Ibrahim *et al*. 2012). Several late Pleistocene fossils from cave sites in peninsular Thailand (Thung Nong Nien, Moh Khiew I, II and Lang Rongrien) were also identified as *Cervus unicolor* (Auetrakulvit 2004).

Palawan island is considered part of the Sundaic biogeographic region as well (Reis & Garong 2001). The Pleistocene fossil record in Palawan goes back to the late Pleistocene in Tabon (Fox 1970) and Ile cave (Piper *et al.* 2011) and contains fossils of two deer species, namely *Axis* (*Hyelaphus*) *calamianensis* and a larger species identified as *Cervus* (*Rusa*) sp.

<Table 3>

3. Materials and methods

Identification criteria for some Pleistocene Cervini have been based on slight morphological and metric differences, supported by limited sample sizes. A more extensive morphometric analysis of deer fossils may confirm whether or not some of the proposed size differences between species are still valid when compared to a larger dataset. Qualitative or non metric definition of morphological characters is inherently subjective to a certain extent (Degusta & Vrba 2005) and since morphological differences between Southeast Asian deer species are particularly subtle, linear- and geometric morphometrics were deemed appropriate complementary techniques to assess whether observed

morphological differences can be quantified. Table 3 gives an overview of the analyzed fossil species with comments on their validity and hypothesized taxonomic status. All the analyzed fossil taxa come from Java and Sumatra.

More specifically, a comparative morphometric study of recent and fossil Cervini was performed on the upper- and lower third molars. We chose to focus on teeth, as these elements often retain their integrity after deposition (Albarella *et al*. 2009). This is even more so the case in Southeast Asian Pleistocene deposits, where osseous material is often reduced to dental remains due to rodent-(*Hystrix* sp.) gnawing (de Vos 1983, Bacon *et al*. 2008). Besides that, teeth are more helpful in taxonomic studies than postcranial elements as they are usually conservative in their structure (Degerbol 1963, Payne & Bull 1988) and furthermore they allow for large modern samples, because museum collections are often composed of skulls rather than complete skeletons.

The third molar was considered to be particularly useful because it suffers less from interproximal abrasion than the other molars (Cucchi *et al*. 2009). In addition, the *lower* third molar has the advantage that it is easily identifiable even if found in an isolated state. Therefore two approaches were taken: a linear morphometric approach on the lower m3 and a geometric morphometric analysis of the upper M3.

3.1 Materials

A total number of 283 fossil specimens were measured at Naturalis in Leiden and 33 specimens were photographed at the same institute for geometric morphometric analysis. Additionally, an extra 25 fossil molars were measured at the Indonesian Center for Geological survey, Bandung. A few measurements were taken from the literature (Bouteaux 2005,), while those from the Pleistocene of Laos and Vietnam were provided by A.M. Bacon and her collaborators (Bacon *et al*. 2008a, 2008b and unpublished data).

As the absolute dating of many of these fossils as well as the sites they come from is controversial (e.g. Indriati *et al*. 2011) and beyond the scope of this paper, we only give a broad indication of the age when discussing individual sites. The material from Bumiaju, Trinil, Kedung Brubus, Sangiran, Ngebung and Ngandong is of Early – Middle Pleistocene age (de Vos *et al*. 1982, de Vos 1985, van den Bergh *et al.* 2001, Bouteaux 2005). Wajak (Storm *et al*. 2013), Punung, (de Vos *et al*. 1982, de Vos 1985, Storm 1995, van den Bergh *et al.* 2001), the Sumatran Cave assemblages (de Vos 1983), Tam Hang (Bacon *et al.* 2008a) and Duoi U'oi (Bacon *et al.* 2008b) are of Late Pleistocene age.

Linear- (128 specimens) and geometric morphometric data (81 specimens) on recent deer were collected at the following institutes: the Natural History Museum of Rotterdam, the National Museums of Scotland, the British Museum of Natural History, the National Museum of Natural History Paris, the Royal Belgian Institute of Natural Sciences, the Zoological Museum University Ghent, the Swedish Museum of Natural History, the Morphology Museum University Ghent and the osteological reference collections of the universities of Durham and Lille. Sample sizes for some species are very low due to their extreme rareness in museum collections. Table 4 provides an overview of the number of specimens collected for each species.

Pathological specimens were systematically excluded and teeth with a severe degree of attrition, which complicated the placement of landmarks, were avoided in the geometric morphometric analysis. Right molars were photographed for gmm-analysis, but a number of left ones were virtually mirrored using TPSdig 2.16 and included in this study as well. Although captivity is known to affect morphology in certain mammals (O'Regan & Kitchener 2005), due to the scarcity of some species in museum collections, zoo specimens were also included to maximize sample size. A table with the original measurements taken by the authors has been provided in appendix A (fossil specimens) and appendix B (extant specimens).

<Table 4>

295 **3.2 Methods**

296 **3.2.1 Linear morphometrics**

297 As a first approach to address these issues, a linear morphometric analysis was applied on a set of
298 fossil deer teeth in addition to a number of recent deer specimens. Measurements of maximum
299 length and width were taken with calipers following Heintz (1970) and expressed in millimeters. The
300 resulting data was plotted on a XY-graph using PAST 2.17b. Inter-rater reliability was tested on a
301 small sample (N=14) of *A. lydekkeri* specimens. Measuring differences were visually assessed using a
302 Bland-Altman plot (Bland and Altman 1986). Although relatively simple, ratios between linear
303 measurements have been successfully applied on cervid fossils as a means to discriminate between
304 taxa (e.g. Heintz 1970, Bouteaux 2005, Castanos *et al*. 2006, 2012, Liouville 2007, Lister *et al*. 2010).
305 Statistical significance between groups was assessed using a Multivariate Analysis of Variance
306 (MANOVA) in PAST 2.17b. As molar measurements are not thought to be substantially affected by
307 sexual dimorphism in other ungulates (Payne & Bull 1988, Kusatman 1991), both male and female
308 individuals were combined in the dataset to ensure a maximum sample size. The majority of the
309 measurements are original, with the exception of the *Axis* sp.-specimens from Ngebung and the
310 *Cervus unicolor* specimens from mainland Southeast Asia.

311 **3.2.2 Geometric morphometrics**

312 Alongside a traditional morphometric approach, a number of teeth were also analyzed using
313 geometric morphometrics (GMM). Previous research on ungulate remains (e.g. Cucchi *et al* 2009,
314 2011., Evin *et al*. 2013a, 2013b, Brophy *et al*. 2014) has shown that digital image analysis of dental
315 morphology can be used to study phenotypic diversity. The drawback of selecting the upper third
316 molar for analysis is that, opposed to the lower third molar, it can be confused with the second- or
317 even the first molar when found in an isolated state. Despite these complications, we chose the
318 upper M3 because it was more prevalent in museum collections (crania are more common than
319 mandibles) and because our preliminary studies on the lower molars provided less promising results.

320 This was possibly in part due to the lack of useful homologous traits that could be easily landmarked.
321 Therefore a method was developed to quantitatively differentiate upper molars based on a ratio
322 between their anterior and posterior width (fig. 3). This was based on the observation that the
323 difference in width between the paracone and protocone (anterior width, AW) becomes increasingly
324 larger relative to the difference in width between the metacone and hypocone (posterior width, PW),
325 from the first to the third upper molar. Based on this ratio an attempt was made to identify
326 individual molars. Using this method on fossil teeth, a number of third molars was selected that
327 could be used for further analysis.

328 <Fig. 3>

329 The advantage of using geometric morphometrics is that size can be analyzed separately from shape
330 (Viscosi & Cardini 2011). It also has the ability to analyze anatomical elements as whole units instead
331 of a number of independent measurements (Zelditch et al. 2004, Curran 2009). As size has often
332 been a criterion used to assign fossil cervids to specific taxa, an independent approach was also
333 considered a useful way to test how well taxonomy is reflected by size differences.

334 Therefore the first part of this analysis was to test on a reasonably large sample if the upper M3 can
335 be used to differentiate deer at species level and to assess whether morphological differences reflect
336 a taxonomic signal. In the second phase a number of Pleistocene fossils were included and compared
337 to the dataset of recent species.

338 Morphological variation in the molars was quantitatively analyzed using a geometric morphometric
339 model where shape was defined by placing a series of homologous landmarks at discrete anatomical
340 loci on the individual teeth (Zelditch *et al*. 2004). The resulting Cartesian coordinate data were, after
341 the appropriate transformations, compared with PAST 2.17b.

342 Using a Nikon D90 camera, photographs were taken of the molars from the occlusal perspective.
343 Teeth were fixed with plasticine on a supporting platform and leveled using a spirit level. The buccal

wall was systematically placed at a 90° angle with the supporting platform and the camera was positioned at 27 cm from the object while focusing on the junction between the enamel and the root.

A total number of 13 landmarks were placed along the outline of the protoconid and hypoconid using TPSdig 2.16 (Rohlf 2004) (fig. 4). Landmarks were only placed on those parts of the molar that were not subject to tooth wear to avoid measuring age-related shape differences. The analysis made use of a combination of type 1- and type 2- landmarks and a series of sliding semilandmarks. Type 1 landmarks have the strongest homology and are defined as locations where multiple discrete tissues intersect at a single point (Baab 2012). Type 2 landmarks have no true biological correspondence, but an emulated homology is supported by the geometry of the surrounding anatomy (Baab 2012). In semilandmarks only the wider structure or surface where the landmarks are positioned is homologous (Baab 2012).

<Fig. 4>

Only landmark III can be defined as a type 1 landmark. Landmark II is defined as the most extreme point of the protoconid, while landmark I is placed at distance x from landmark II on the anterior portion of the outline, where x equals the linear distance between landmark II and III. Landmark IV is defined at the same distance (x) from landmark III along the outline of the hypoconid. As these three landmarks only have a geometric correspondence, they can be described as type II landmarks. In addition three series of semilandmarks were placed in between these four type I/II landmarks.

Given the inherently arbitrary location of the semilandmarks, additional treatment was needed to improve the one to one correspondence of these points (Bookstein 1997). Using TPSrelw 1.49 (Rohlf 2005) semilandmarks were slid along homologous curves between the above mentioned type 1 and type 2 landmarks (Bookstein 1997). The *minimize procrustes distance*-option was used as a sliding method. This procedure removes the difference along the curve in semilandmark positions between

368 the reference form and the individual specimens by estimating the direction tangential to the curve
369 and removing the component of the difference that lies along this tangent (Sheets *et al*. 2004).

370 Besides that, TPSrelw was also used for a generalized procrustes superimposition of the complete set
371 of landmarks. By overlaying homologous landmarks and minimizing procrustes distances (Goodall
372 1991), objects were scaled, rotated and translated to exclude information that is irrelevant to
373 differences in shape (Walker 2000). During the generalized procrustes superimposition shape
374 coordinates are projected in a euclidian space tangent to the procrustes shape space (Viscosi &
375 Cardini 2011). Whether this approximation in tangent space is good enough for further statistical
376 analysis was tested with TPSSmall 1.20 (Rohlf 2003) on a procrustes datamatrix with all specimens
377 included.

378 To assess the repeatability of the digitization protocol, six specimens were randomly photographed
379 and landmarked five times using the same standardized protocol. This test was based on the protocol
380 by Adriaens (2007) and was performed to evaluate whether the used methodology allows for any
381 significant errors to occur during the digitization process of the landmarks (Cucchi *et al*. 2011). When
382 performing a principle components analysis (PCA) on these five replicates, the same individuals are
383 expected to cluster together.

384 PAST 2.17b (Hammer *et al*. 2001) was used for all statistical analyses of the resulting coordinate data.
385 Several multivariate analyses were performed to explore morphological variation in cervid molar
386 shape. Principle component analysis (PCA) was primarily used to explore how species clustered
387 together in groups and to reduce the amount of variables for potential further analysis. All shape
388 variables were included in order to identify the greatest axes of molar shape variation in the dataset
389 (Cucchi *et al*. 2011). Shape changes along the axes of the different relevant components were
390 visualized using thin plate spline deformation grids. A permutational multivariate analysis of variance
391 (NPMANOVA) was run on the most relevant principle components to determine statistical
392 significance between designated groups. Further, a Canonical Variates Analysis (CVA) was run on

393 certain selected groups to maximize the between groups variability, to test the significance of shape
394 differences and to determine the relationships between different species.

395 Although the generalized procrustes analysis excludes all size differences, it does not eliminate the
396 effects of allometry (Curran 2009). Therefore, the results of the relevant components were regressed
397 against log centroid size to test whether there was a correlation between size and shape.

398 **4. Results**

399 **4.1 Linear morphometric analysis**

400 A visual inspection of a Bland-Altman plot of mean differences in measurement (not shown)
401 suggested there was no consistent bias between observers. In fig. 5 linear measurements are plotted
402 of the maximum length and width of fossil deer teeth from Java. Although subtle morphological
403 differences are not taken into account here, several conclusions can be drawn from the data in
404 relationship to what is known from the literature. The Pleistocene *Axis lydekkeri* (open squares) are
405 clearly the smallest species known from the fossil record. Although there is slight overlap with the
406 fossil *Cervus kendengensis* specimens (stars) from the collection in Leiden, both species separate
407 reasonably well in different clusters and the results of a MANOVA (table 5) indicate a significant
408 difference (p<0.001). The clusters suggest a disparity between at least a larger form and smaller form
409 in the fossil record.

410 In a comparison in figure 7 of *Axis lydekkeri* (open squares) with the living members of the genus
411 *Axis*, it appears to overlap with both *Axis* (*Hyelaphus*) *kuhlii* (dots) and *Axis* (*Hyelaphus*) *porcinus*
412 (open diamonds), but is generally smaller than the Indian *Axis* (*Axis*) *axis* (crosses). The MANOVA
413 (table 5) however indicated not only significant differences between *A. lydekkeri* and *A. axis*
414 (p<0.001), but also between *A. lydekkeri* and *A. porcinus* (p=0.010). Differences between *A. lydekkeri*
415 and *A. kuhlii* were not significant (p=0.467).

Comparing *Axis javanicus* (vertical rectangles) with the other paleospecies (fig. 5), it becomes clear that, although placed under the genus *Axis*, it does not cluster well with the smaller specimens in our dataset, and is more similar in size to the (presumed) *Rusa* deer like *Cervus kendengensis* (p=0.079, stars). This is confirmed by comparison with measurements of recent Southeast Asian species (fig. 6). *A. javanicus* falls within the range of the living *Cervus* (*Rusa*) *timorensis* (p=0.687, filled squares).

When on the other hand, the measurements of *A. javanicus* are plotted against the measurements of extant deer from the genus *Axis* (Fig. 7), it becomes clear that *Axis javanicus* (vertical rectangles) is significantly larger than *Axis* (*Hyelaphus*) *porcinus* (p=0.002, open diamonds) and the fossil *Axis lydekkeri* (p<0.001, open squares), but falls well within the size range of the living Indian *Axis* (*Axis*) *axis* (p=0.100, crosses).

<Table 5>

<Fig. 5>

<Fig. 6>

<Fig. 7>

<Fig. 8>

Cervus zwaani (fig. 5, filled diamonds) appears to be part of the cluster of smaller species. From comparison with the other small paleospecies from Java and extant members of the genus *Axis* (fig. 7), it appears to be similar in length to the other Axis deer, yet somewhat wider. The MANOVA (table 5) suggests it is significantly different from *Axis lydekkeri* (p<0.001, open squares), recent *Axis* (*Axis*) *axis* (p<0.001, crosses) and *Axis* (*Hyelaphus*) *porcinus* (p=0.042, open diamonds), but not from the *Axis* sp. specimens from Ngebung. According to von Koenigswald (1933) its teeth are supposedly larger and more robust than those of *A. lydekkeri*. But Zaim *et al*. (2003) pointed out, this size difference is not confirmed by comparative measurements with *A. lydekkeri*. Although the third

439 molar may be slightly more robust, there is considerable visual overlap in size between the two
440 forms. The *Axis* sp. specimens from the Pleistocene site of Ngebung (fig. 7, filled triangles) are not
441 significantly different from *Axis lydekkeri* (p=0.365). Although *Cervus oppenoorthi* (not in the graphs)
442 cannot be ruled out as another candidate for *Axis* sp., it was impossible to include this species in the
443 analysis due to the fact that it is only known from antler fragments.

444 When comparing the larger Javanese deer with living representatives of the subgenus *Rusa* (fig. 6), it
445 becomes clear that there is size overlap between the several different groups. *Cervus kendengensis*
446 (fig. 6, crosses) was considered by Dubois to be comparable in shape to extant *Cervus* (*Rusa*)
447 *timorensis* (Dubois 1908). While the morphometric data (fig.6) does indeed suggest a similarity of this
448 form to the subgenus *Rusa*, the visual overlap with recent *Cervus* (*Rusa*) *timorensis* (filled squares) as
449 well as with the living *Cervus* (*Rusa*) *unicolor* (open squares) complicates interpretation. That size
450 may not be a good indicator for taxonomic differences between *Rusa*-species, is also suggested by
451 limited metric differences between fossil- (inversed filled triangles) and recent *Cervus* (*Rusa*)
452 *timorensis* (filled squares).

453 The fossil *Cervus stehlini* (fig. 6, ellipses) was another species considered by von Koenigswald (1933)
454 to be closely related to *Cervus* (*Rusa*) *timorensis* (filled squares), which is confirmed by our linear
455 morphometric data. *C. stehlini* is not significantly different from extant *C. timorensis* (p=0.685) and
456 fossil *C. timorensis/hippelaphus* (p=0.080), but is from C. unicolor (p<0.001). Von Koenigswald (1933)
457 recognized it as a separate species, mainly due to its particularly slender premolars. Even though the
458 premolars of this species were not included in this analysis, it should be noted that the lower third
459 molar is not particularly slender and can even be said to plot out between the rather robust teeth
460 within the extant *Cervus* (*Rusa*) *timorensis*-group.

461 *Cervus* (*Rusa*) *problematicus* (fig. 6, cross) is clearly much larger than any of the known fossil- or
462 recent Javanese deer. It falls within the spectrum of extant *Cervus* (*Rusa*) *unicolor* (open squares), but
463 whether it should be considered synonymous is unclear.

In fig. 8 measurements of Pleistocene *Cervus* (*Rusa*) sp. from Sumatra (open triangles) have been plotted against recent members of the subgenus *Rusa* and fossil *Cervus* (*Rusa*) *unicolor* from Tam Hang, Laos (Bacon *et al*. 2008a, Bacon *et al*. unpublished data, dots), Duoi Uoi, Vietnam (Bacon *et al*. 2008b; Bacon *et al*. unpublished data, filled triangles) and Lang Trang, Vietnam (Long *et al*. 1996, stars). Again the data indicate that caution is advised when using size to differentiate between *Rusa*-deer. The measurements from Duoi Uoi suggest a wider size range in fossil *Cervus* (*Rusa*) *unicolor* than what would have been expected from the recent *C. unicolor* sample (open squares). This is evidently based on the assumption that the fossils from Duoi Uoi should indeed all be placed under this species. Nevertheless the *Cervus* (*Rusa*) sp. sample from Sumatra (open triangles) is clearly larger than the living *Cervus* (*Rusa*) *timorensis* (p<0.001,filled squares) and the Phillipine Rusa species, *Cervus* (*Rusa*) *alfredi* (p<0.001, circles) and *Cervus* (*Rusa*) *mariannus* (p<0.001, horizontal rectangles). *Cervus* (*Rusa*) sp. (open triangles) on the other hand overlaps more with recent *Cervus* (*Rusa*) *unicolor* (open squares), the larger *C. unicolor* specimens from the Pleistocene Duoi Uoi (filled triangles) and fossil *C. unicolor* from Lang Trang (stars) and Tam Hang (dots). The MANOVA however suggested significant differences between *Cervus* sp. and these three forms (all p<0.001).

4.2 Geometric morphometric analysis

In figure 9 the results of our metric analysis of the relative size of the anterior and posterior part of the upper molars are shown. The data point out that there was overlap between the first (green crosses) and the second molar (blue squares) and between the second- and the third molar (red crosses). Nevertheless the size difference between the anterior and posterior part was more pronounced in the third molar and therefore separated reasonably well on the y-axis. A Mann-Whitney *U*-test on the tooth index values showed the separation between m2 and m3 was statistically significant (p<0.001), allowing separation of the teeth. In addition to morphological criteria we identified those molars with an index of at least 120 ([anterior width/posterior width] x 100) as upper M3s.

From our analysis in TPSSmall it can be concluded that the projection of our shape coordinates in tangent shape space is good enough for further statistical analysis (slope=0.998153 and p=1). The repeatability test (fig. 10) revealed that although there was limited error in the digitization process, the clustering together of replicates indicates that the variation caused by digitization error was not too large to obscure natural shape variation.

<Fig. 9>

<Fig. 10>

A PCA of the set of 13 landmarks (fig. 11), gives limited but visual separation between certain species or groups of species. The first two components (PC1 and PC2) together explain the majority (81%) of the total variation in the dataset (table 6). The broken stick model distribution on eigenvalues suggested only the first two components were significant. Because of this reason, and because it provided the best visual separation, only the first two components were used in this analysis and visualized in figure 11. In the thin plate spline deformation grids at both ends of the two axes an idea is given of the morphological changes described by the first two components. Shape changes along the axis of PC1 can be interpreted as a change in the angle of the hypoconid relative to the protoconid. Changes along the axis of PC2 can be explained as the general development- and difference in pointiness- of the hypoconid and protoconid (fig. 11).

The results of a permutational MANOVA run on the scores of the relevant principle components (PC1 and PC2 as indicated by a broken stick model distribution of eigenvalues) explaining together 81.1 % of the total variation, is given in table 7. Although visual separation was not clear between all groups in the initial PCA, in the permutational MANOVA the distinction was statistically significant between different clusters (p<0.001). Non-significant differences (non-bold values in table 7) between individual species may be due to natural similarities between groups, but also because of the small sample sizes for certain taxa (*Axis lydekkeri, Axis kuhlii, Cervus mariannus* and *Cervus alfredi*) or the limited area of the teeth that was quantified.

514 To test whether the shape differences summarized in the first two components were correlated with
515 size, the scores of PC1 and PC2 were regressed against centroid size. The results point out that there
516 was a weak correlation between size and the first component (r=0,446), suggesting that a small part
517 of the shape variation in PC1 may be picking up an allometric signal. However, when removing the
518 largest species from the sample (*Cervus unicolor*, *Elaphurus davidianus* and Sumatran *Cervus* sp.), the
519 correlation coefficient becomes considerably smaller and negative (r=-0,143). This suggests that if
520 shape differences in PC1 are partially explained by allometry, these differences are primarily driven
521 by the largest species in the sample. No significant correlation was observed between the second
522 component and size (r=0,014).

523 <Fig. 11>

524 <Table 6>

525 <Table 7>

526 In the PCA with all specimens included, the living members of the subgenus *Hyelaphus* (*A. kuhlii*
527 (large crosses) and *A. porcinus* (open diamonds)) are clearly separated from recent *Axis* (*Axis*) *axis*
528 (small crosses) on PC1 (fig. 11). The permutational MANOVA (table 7) indicates these differences are
529 highly significant (p=0.0095, p<0.001). Although in the taxonomic scheme followed in this paper
530 (Groves and Grubb 1987), *Hylaphus* and *Axis* are placed together under the same genus (*Axis*), it is
531 not unlikely that these scores reflect a true phylogenetic difference. As already mentioned, more
532 recent molecular and morphological studies (Pitra *et al*. 2004, Meijaard and Groves 2004) have
533 argued that *Hyelaphus* may not be closely related to *Axis* and should perhaps be placed closer to the
534 subgenus *Rusa*.

535 In addition, the fossil *Axis lydekkeri* (dots) also grouped together with the two species of the
536 subgenus *Hyelaphus* (open diamonds and large crosses) in the PCA (fig. 11). Differences between *A.*
537 *lydekkeri*, *A. porcinus* (p=0.3334) and *A. kuhlii* (p=0.4902) were not significant. This is in agreement

538 with the conclusions by Meijaard and Groves (2004) that *Axis lydekkeri* should be placed under the
539 (sub)genus *Hyelaphus* and not *Axis*. These shape differences are not thought to be size related, as no
540 allometric effect was observed in PC1 and PC2 amongst the smaller sized species. Due to the fact that
541 different species within the *Hyelaphus* group overlapped and because of the small sample size, it was
542 not possible to get a better insight into the relationships between *A. lydekkeri*, *A. porcinus* and *A.*
543 *kuhlii*.

544 Members of the subgenera *Cervus* (vertical rectangles), *Rucervus* (inversed triangles) and *Rusa*
545 (squares, filled triangles and filled diamonds) did not separate well on PC1 (fig. 11) and, as suggested
546 from the regressions, a limited allometric effect may be present for the larger species within these
547 groups. There is, on the other hand, some weak separation on PC2. The proximity of these subgenera
548 in morphospace (fig. 11) suggests a close similarity between *Cervus* s.s. and *Rusa*, which is supported
549 by the molecular studies by Pitra *et al*. (2004). *Elaphurus davidianus* (horizontal rectangles) scores
550 highest on PC1, but as this is the largest species in the sample, caution is urged due to the possibility
551 of a limited allometric effect as suggested by the regressions against centroid size. Within the
552 subgenus *Rusa* (squares, filled triangles and filled diamonds), there is overlap in the PCA (fig. 11)
553 between all species with the exception of *Cervus* (*Rusa*) *alfredi* (filled triangles). On the vertical axis
554 (PC2) *Cervus* (*Rusa*) *timorensis* (filled squares) scores generally higher than *Cervus* (*Rusa*) *unicolor*
555 (open squares) but there is overlap in the center. The fossil *Cervus kendengensis* (circles) groups
556 reasonably well with *Cervus* (*Rusa*) *timorensis* (filled squares), but also to a limited extent with *Cervus*
557 (*Rusa*) *unicolor* (open squares). The permutational MANOVA (table 7) however pointed out that both
558 *C. kendengensis* and *C. timorensis* are significantly different from *C. unicolor* (p=0.0001, p=0.0082)
559 but not from each other (p=0.2524).

560 Although in the linear morphometric analysis (fig. 8) the Pleistocene *Cervus* (*Rusa*) sp. from Sumatra
561 (open triangles) appears to be clearly larger in size than *Cervus* (*Rusa*) *timorensis* (filled squares), in
562 the geometric morphometric analysis it overlaps with *Cervus* (*Rusa*) *timorensis* (filled squares) as well

563 as with the fossil *Cervus kendengensis* (circles) and recent *Cervus* (*Rusa*) *unicolor* (open squares). The
564 permutational MANOVA (table 7) indicated that *Cervus* sp. is significantly different from *Cervus*
565 *unicolor* (p=0.0019) but not from both *Cervus timorensis* (p=0.5149) and *Cervus kendengensis*
566 (p=0.0545).

567 In order to get a better separation between *Rusa* species, a Canonical Variates Analysis (CVA) was run
568 on the first 12 components of the PCA that together summarized 99.6% of the total variance, with
569 only *Cervus kendengensis* (dots), Pleistocene *Cervus* (*Rusa*) sp. from Sumatra (open triangles) and the
570 living members of the subgenus *Rusa* (filled squares, filled triangles, open squares and ellipses)
571 included. The results are plotted out in figure 12. Visual separation between the living species is
572 clearly much better than in the PCA and happens mostly on the horizontal axis.

573 *Cervus kendengensis* (dots) groups closely together with *Cervus* (*Rusa*) *timorensis* (filled squares), and
574 is further removed from the other recent species in morphospace. Contrary to what was suggested
575 by the results of the linear morphometric analysis (fig.11), the fossil *Cervus* (*Rusa*) sp. from Sumatra
576 (open triangles) clearly overlap with *Cervus* (*Rusa*) *timorensis* (filled squares) and not with any of the
577 other living *Rusa*-deer like *Cervus* (*Rusa*) *unicolor* (open squares) or *Cervus* (*Rusa*) *alfredi* (filled
578 triangles). If we consider the percentage of correct reclassifications for the different assigned groups
579 in table 8(a), 42% of the specimens were correctly reclassified to the right species with jackknifed
580 cross-validation. However, when considering *Cervus kendengensis*, *Cervus* (*Rusa*) *timorensis* and
581 *Cervus* (*Rusa*) sp. as a single group (table 8b), 78% of the specimens were correctly reclassified.

582 <Fig. 12>

583 <Table 8 >

584 **5. Discussion and conclusions**

585 The results of the linear morphometric analysis showed considerable overlap between different
586 species and the size range of some species may have been wider in the past than may be expected

587 from their living conspecifics. Nevertheless, some conclusions can be drawn from the results. The
588 linear study included a broader range of fossil species than the geometric morphometric analysis, but
589 both methods provided similar results.

590 It can be concluded from the two methods that both medium- and larger sized deer species are
591 present in the Javanese fossil record. This confirms statements by Martin (1888) and Dubois (1891,
592 1907, 1908) that besides *Axis lydekkeri*, there is also at least one larger form present during the
593 Pleistocene in Java.

594 *Axis lydekkeri*, the best known species, is most similar in shape to *Axis* (*Hyelaphus*) *porcinus* and *Axis*
595 (*Hyelaphus*) *kuhlii*. We therefore follow Meijaard and Groves (2004), in that *A. lydekkeri* should be
596 placed under the subgenus *Hyelaphus*. The results of the geometric morphometric analysis also
597 strongly suggest that the genus *Axis* needs revision and that extant *Axis kuhlii* and *Axis porcinus* may
598 not be closely related to *Axis axis*. While the extinct *A*. *lydekkeri* and recent *A. kuhlii* and *A*. *porcinus*
599 seem closely related, the relationship between these tree species individually is not clear, although
600 linear measurements suggest it is most closely related to *A*. *kuhlii*. This is not unlikely since *A. kuhlii* is
601 still present in Java.

602 The fossil *Axis* sp. from Ngebung is undoubtedly smaller in size than *Axis javanicus*, but falls within
603 the range of *Axis lydekkeri.* Although we cannot exclude its identification as *Cervus oppenoorthi*, we
604 provisionally place it under *Axis lydekkeri*. Contrary to von Koenigswald's (1933) statement, only
605 slight differences in size or robustness were found between *Cervus zwaani* and *Axis lydekkeri*. The
606 linear morphometric analysis suggested some difference between these two, but no significant
607 difference between *C. zwaani* and the *Axis* specimens from Ngebung (who were found highly similar
608 to *A. lydekkeri*). Based on the linear morphometric analysis and given the scant fossil evidence, *C.*
609 *zwaani* should therefore probably be considered a junior synonym of *Axis lydekkeri*, as was suggested
610 by Zaim *et al*. (2003).

Axis javanicus is similar in size to recent *Axis axis* and larger than *Axis kuhlii*, *Axis porcinus* and fossil *Axis lydekkeri*. We consider it a valid species, but whether its closest living relative is *Axis axis* cannot be concluded with certainty from the data. As for *Cervus oppenoorthi*, no conclusions can be drawn about its validity since it was not included in our analysis. From the literature it can be inferred that it is probably related to the *Hyelaphus*-group.

Cervus problematicus was not included in the geometric morphometric analysis, but the clear difference in size from all other known Javanese species suggests it cannot be identified as any of the other known fossil taxa. It is similar in size to the living *Cervus* (*Rusa*) *unicolor*, but in view of the fact that there are no fossil or historical records for this species in Java, we provisionally recognize *C. problematicus* as a valid species.

Cervus (*Rusa*) *stehlini* was considered by von Koenigswald as a separate species from *Cervus* (*Rusa*) *timorensis*, based on the peculiar morphology and slenderness of its premolars (von Koenigswald 1933). Although the species was not included in the geometric morphometric analysis and no premolars were included in this study in general, the lower m3 was not found to be more slender than that of *C. timorensis*. Although its validity could not be refuted with certainty here, we urge for caution when attributing fossils to this taxon. If not synonymous with *C. timorensis*, it is probably closely related to it.

Cervus palaeomendjangan was not included in this study, as it is unclear what specimens Dubois (1908) was referring to when proposing it as a new species. The scant evidence in addition to von Koenigswald (1933) who considered it invalid, imply that it may be a synonym of one of the other species.

As Dubois (1908) already pointed out, *Cervus kendengensis* is similar in shape to *Cervus* (*Rusa*) *timorensis*. He considered it a separate species mainly based on the morphology of the antlers. The linear morphometric analysis confirms its placement under the subgenus *Rusa*. Moreover, the geometric morphometric analysis indicated it is more similar in morphology to *C. timorensis* than to

any of the other living *Rusa* deer. Awaiting further research on e.g. antler morphology we consider it a valid species, though closely related, if not ancestral to the Javanese sambar (*C. timorensis*).

The presence of *Cervus* (*Rucervus*) *eldii* in the Javanese Pleistocene record, though not tested in this study, is considered unlikely. No other records of this species are known from Java or the rest of Sundaland. Moreover, the supposed characteristic morphology of the antler fragment (the angle between the beam and the brown tine) is also reported for other Javanese fossil species (*Axis javanicus*) (von Koenigswald 1933). We regard *C. eldii* as absent from the Javanese fossil record.

The Sumatran Pleistocene deer (*Cervus* (*Rusa*) sp.) clusters with *Cervus* (*Rusa*) *unicolor* when considering size, but the geometric morphometric analysis pointed out its similarity to *Cervus* (*Rusa*) *timorensis* and the fossil species *Cervus kendengensis*. This is surprising, since the majority of the fauna associated with *Cervus* sp. is considered essentially modern (de Vos 1983) and *Cervus* (*Rusa*) *unicolor* is the only deer of the Cervini tribe currently present on Sumatra. If our identifications are sound, there are several possible scenarios for the Pleistocene deer of Sumatra. One possibility is that *Cervus* (*Rusa*) sp. is synonymous with *Cervus* (*Rusa*) *timorensis*, but that its size range was wider in the past. From the measurements on the mainland deer fossils it was already suggested that this was the case with *Cervus* (*Rusa*) *unicolor*. In addition, it should be noted that large sizes were also observed for several other mammal groups found in the Sumatran cave deposits, such as *Symphalangus* (Hooijer 1960), *Pongo* (Hooijer 1948, Harrison 2000) and *Hystrix* (Hooijer 1946). Although there is some debate whether these differences are enough for the recognition of separate subspecies (Badoux 1959, Van Weers 2003), it demonstrates a larger flexibility in size than what may be expected from their living representatives. Likewise, a similar size reduction since the Late Pleistocene was also observed in Borneo for a number of mammals like *Tapirus*, *Pongo*, several cercopithecids and even *Muntiacus* (Medway 1964).

Another possibility is that *Cervus* (*Rusa*) *unicolor* is not monospecific. According to a recent taxonomic revision by Groves (2011), the sambar should be split up in two species: *Cervus* (*Rusa*)

unicolor from Sri Lanka and mainland South Asia and *Cervus* (*Rusa*) *equina* from Southeast Asia and the Indomalayan archipelago. Since a large portion of our *C. unicolor* sample was not provenanced, it is possibly biased towards specimens from the Indian subcontinent (*Cervus/Rusa unicolor unicolor*). If the Indomalayan species *Cervus* (*Rusa*) *equina* is more closely related to *C. timorensis*, as proposed by Groves (2011), this would also have implications for the position of both *Cervus* (*Rusa*) sp. and *Cervus kendengensis* in our analysis as we would have missed a crucial species.

A third possibility is that the fossils from Sumatra belong to an extinct species different from both *Cervus timorensis* and *Cervus unicolor*. In that case the data still suggests that it is most closely related to *Cervus timorensis* and the fossil *Cervus kendengensis*.

6. General conclusion

This attempt to shed new light on the taxonomic relationships between the Pleistocene Cervini from Java and Sumatra, has resulted in some novel insights. Although our study was hampered by difficulties such as the inaccessibility of some material and the fact that certain species are only known from antler fragments, our results show that a combination of linear- and geometric morphometrics can be used to gain a better understanding of Southeast Asian deer taxonomy.

This quantitative approach was deemed especially helpful in a group of fossil mammals, where different taxa have traditionally been separated based on subtle and often subjective, qualitative criteria. However, in order to construct a more conclusive taxonomic review there are several problems to overcome. Firstly, a thorough and conclusive revision of the taxonomy and phylogeny of recent Cervini is needed, which can then be used as a reliable baseline for further paleontological research. Besides that, there is a need to apply similar methods to other deer elements and species from fossil collections in Java and Sumatra, and ideally also from the Asian mainland. This is especially the case for antlers as several Pleistocene deer have been placed in separate taxa because of their particular antler morphology. As a third note, we argue for a better understanding of body size variability in living and fossil deer and how this is reflected in tooth size.

686 Ultimately, a more complete and integrated knowledge of Southeast Asian fossil and living cervid
687 taxonomy and evolution should lead to a better understanding of the changing environmental
688 conditions that were present in Southeast Asia during the Quaternary. This in turn could be linked
689 with other palaeoecological datasets and contribute to the understanding of our own genus' ecology
690 in Eurasia during the Pleistocene and Holocene.

691 **Acknowledgements**

692 The authors would like to thank the curators and collection managers who facilitated our data
693 collection: Reinier van Zelst, Henry van der Es, Andrew Kitchener, Zena Floody, Joséphine Lesur,
694 George Lenglet, Sebastien Bruaux, Dominique Verschelde, Daniela Kalthoff, Marjan Doom, Fachroel
695 Aziz and Andy Currant. Our gratitude also goes to Tarek Oueslati, Una Strand-Vidarsdottir and Sarah
696 Elton for their insights and to the reviewers for their helpful comments. We are especially grateful to
697 Anne Marie Bacon, Vu The Long, Nguyen Thi Kim Thu and Thongsa Sayavongkhamdy for providing us
698 with the measurements from Duoi U'oi and Tam Hang.

699

700 **Figures**

701 *Fig. 1: map of Sundaland during the last glacial maximum (adapted from Bird et al. 2005)*

702 *Fig. 2: Map of Asia with distribution of recent Cervini included in this analysis. The Western*
703 *distribution of red deer (Cervus elaphus) in North Africa, Europe and North America and that of fallow*
704 *deer (Dama dama) in Europe, is not illustrated. (1=Dama dama, 2=Elaphurus davidianus, 3=Axis axis,*
705 *4=Cervus alfredi, 5=Axis kuhlii, 6=Cervus timorensis, 7=Cervus unicolor, 8=Cervus elaphus, 9=Rucervus*
706 *eldii, 10=Axis porcinus, 11=Rucervus duvaucelli, 12=Cervus mariannus, 13=Axis calamianensis).*
707 *Species distributions are based on van Bemmel (1949), Corbet (1978,) Chapman and Chapman (1980),*
708 *Groves (1982), Cao (1993) and Grubb (2005)*

Fig. 3: Anterior width (AW) and posterior width (PW) measurements on the upper M3, adapted from Lister (1996).

Fig. 4: Positioning of landmarks on the upper third molar. I to IV are type 2 landmarks, 'a' to 'i' are type 3 landmarks.

Fig. 5: Length and width measurements of fossil lower m3s from Java. "f"= fossil C.hippelaphus/timorensis

Fig. 6: Length and width measurements of Javanese fossil- and recent lower m3s of the (supposed) subgenus Rusa. "f"= fossil C.hippelaphus/timorensis

Fig. 7: Length and width measurements of fossil and modern lower m3s of the (supposed) genus Axis.

Fig. 8: Length and width measurements of lower m3s of extant members of the subgenus Rusa, fossil Cervus (Rusa) unicolor from mainland Southeast Asia and fossil Cervus (Rusa) sp. from Sumatra.

Fig. 9: Ratio of the relative width of the anterior and posterior part of the upper M3 against molar length for recent specimens (AW=anterior width; PW= posterior width)

Fig. 10: results on PC1 and PC2 of PCA repeatability test on random specimens (1 specimen=1 color/symbol)

Fig. 11: PCA of all deer teeth (first two components). Shape changes along the axes of PC1 and PC2 are visualized with thin plate spline deformation grids showing hypothetical extreme values at the end of each axis.

Fig. 12: CVA of first twelve principle components for Cervus kendengensis, Cervus (Rusa) timorensis, Sumatran Cervus (Rusa) sp., Cervus (Rusa) mariannus, Cervus (Rusa) unicolor and Cervus (Rusa) alfredi.

Tables

Table 1: Taxonomic scheme used in this paper, based on Groves and Grubb (1987)

Table 2: Taxa known from the Javanese Pleistocene

Table 3: Fossil species included in our analysis and hypotheses that were tested.

Table 4: Overview of species used in morphometric analysis.

Table 5: p-values of MANOVA on length and width measurements of the m3, with significant values (p<0.05) in bold (C. problematicus excluded as N=1).

Table 6: Variance explained by principle components 1 to 26.

Table 7: p-values of permutational MANOVA of the first two principle component scores, with significant values (p<0.05) in bold.

Table 8(a and b): Cross-validation results for the CVA on (supposed) Rusa-members with number of reclassifications and reclassification percentages in parenthesis. Lower table with C. kendengensis, Cervus (Rusa) sp. and Cervus (Rusa) timorensis as one group.

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Table 1

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Genus	Species	Included/ not included in this analysis	Subgenus	Comments
Genus Axis	Chital (*Axis axis*)	Included	*Axis*	The subgenus *Axis* consists of only one species (*A. Axis*) and the subgenus *Hyelaphus* of three (*A. kuhlii, A. calamianensis* and *A. porcinus*). Morphological (Meijaard & Groves 2004) and molecular research (Pitra et al. 2004) support a relationship between the members of *Hyelaphus*, but *Axis axis* may not be closely related to this subgenus (Meijaard & Groves 2004).
	Bawean deer (*Axis kuhlii*)	Included	*Hyelaphus*	
	Calamian deer (*Axis calamianensis*)	Not included	*Hyelaphus*	
	Hog deer (*Axis porcinus*)	Included	*Hyelaphus*	
Genus Dama	Fallow deer (*Dama dama*)	Included	*Dama*	The divergence of *Dama, Axis* and *Cervus* is not well known. Emmerson & Tate (1993) suggest a close relationship with *Axis axis*, while Di stephano & Petronio (2002) argue for a Pleistocene split from the *Cervus-Ruso* lineage. According to some authors (Groves 2007) the subspecies *D. dama mesopotamica* should be considered a distinct species.
Genus Cervus	Red deer (*Cervus elaphus*)	Included	*Cervus*	According to the molecular study by Pitra et al. (2004) *Cervus elaphus* may not be monophyletic. The Central Asian- and the North African red deer should possibly be regarded as separate species, while the Central- and East Asian group is placed together with the North American wapiti under the species *Cervus canadensis*.
	Sika deer (*Cervus nippon*)	Not included	*Cervus*	Sika might be closely related to the East Asian red deer/wapiti (Pitra et al. 2004)
	White-lipped deer (*Cervus albirostris*)	Not included	*Przewalskium*	White-lipped deer may be a sister species to the Wapiti/Shou/Sika group (Pitra et al. 2004)
	Eld's deer (*Cervus eldi*)	Included	*Rucervus*	While tentatively placed under the subgenus *Rucervus*, both molecular (Pitra et al. 2004) and morphological data (Groves 2007) suggest a separate genus: *Panolia*.
	Barasingha (*Cervus duvaucelii*)	Included	*Rucervus*	Molecular data (Pitra et al. 2004) suggests *C. Duvaucelii* and *C. Schomburgki* are most closely related to *Axis axis*, but differences are large enough to retain two separate genera (*Axis* and *Rucervus*)
	Schomburgk's deer (*Cervus schomburgki*)	Not included	*Rucervus*	
	Sambar (*Cervus unicolor*)	Included	*Ruso*	*Cervus timorensis* and *Cervus unicolor* may be closely related to the subgenus *Hyelaphus* (Pitra et al. 2004)
	Javan rusa (*Cervus timorensis*)	Included	*Ruso*	
	Philippine spotted deer (*Cervus alfredi*)	Included	*Ruso*	Craniometric research suggests a similarity between *Cervus alfredi* and *Cervus mariannus* but both may be distinct from *Cervus timorensis* and *Cervus unicolor* (Meijaard & Groves 2004).
	Philippine deer (*Cervus mariannus*)	Included	*Ruso*	
Genus Elaphurus	Père David's deer (*Elaphurus davidianus*)	Included	*Elaphurus*	Morphological- (Meijaard & Groves 2004) and molecular data (Pitra et al. 2004) support a separate genus, but the identity of its closest relatives remains uncertain. Possibly this species resulted from hybridisation between two species (Groves & Grubb 1987). Others argue for a fusion of the (sub-)genus with Rucervus (Randi et al. 2001)

Table 2

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Species	Synonyms
Axis Lydekkeri (Martin 1886)	*Cervus lydekkeri* (Martin 1886, Vogel von Falkenstein 1910) *Axis axis* (Dubois 1891) *Cervus liriocerus* (Dubois 1907, 1908) *Cervus (Axis) lydekkeri* (Stremme 1911, Stehlin 1925, Von Koenigswald 1933, 1934)
Axis javanicus (Von Koenigswald 1933)	*Cervus javanicus* (Von Koenigswald 1933,1934) *Axis sunda* (Kretzoi 1947)
Axis (Hyelaphus) kuhlii (Temminck 1836)	*Cervus kuhlii* (Haltenorth 1963)
Cervus zwaani (Von Koenigswald 1933)	Possibly junior synonym of *Axis lydekkeri* (Martin 1886)
Cervus (Rusa) stehlini (Von Koenigswald 1933)	None known
Cervus oppenoorthi (von Koenigswald 1933)	According to Van Bemmel (1944) a junior synonym of *Axis (Hyelaphus) kuhlii*
Cervus (Rusa) timorensis (de Blainville 1822)	*Cervus hippelaphus* *Cervus russa* *Cervus unicolor russa*
Cervus kendengensis (Dubois 1908)	Unknown
Cervus palaeomendjangang (Dubois 1908)	Possibly junior synonym of *Cervus kendengensis* (Von Koenigswald 1933)
Cervus problematicus (von Koenigswald 1933)	Unknown
Cervus sp. (Martin 1888)	Unknown
Cervus (Dubois 1907)	Unknown
Cervus (Rusa) sp. (Dubois 1892)	Unknown
Cervus (Rusa) sp. (Von Koenigswald 1933)	Unknown
Cervus sp. (Stehlin 1925)	Unknown
Cervus sp. (Von Koenigswald 1933)	Unknown
Cervus (Rusa) sp. (Aziz & De Vos 1999)	Unknown
Cervus sp. (Stehn & Umgrove 1926)	Unknown

Table 3

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Fossil species/ specimens	Subgenus	Included/ not included in linear morphometric analysis	Included/ not included in geometric morphometric analysis	Comments and tested hypotheses (in parenthesis)
Axis lydekkeri	*Hyelaphus* ?	Included	Included	According to Meijaard & Groves (2004) this species belongs to the (sub-) genus *Hyelaphus*. In addition this subgenus may not be closely related to *Axis*, and should possibly be considered a separate genus. Based on comparative measurements Zaim et al. (2003) argued that this species may be a senior synonym of *Cervus zwaani*. (Is *Axis lydekkeri* a synonym of *Axis zwaani* or perhaps other species? How is *Axis lydekkeri* related to the modern members of the genus *Axis* ?)
Axis javanicus	*Hyelaphus* ? *Axis* ?	Included	not included	This species could be closely related or even synonymous to *Axis axis* (Meijaard & Groves 2004). (Is there reason to assume *A.javanicus* is a separate species?)
Axis sp. (Ngebung)	*Hyelaphus* ? *Axis* ?	Included	not included	A small sample of cervid teeth were identified as Axis sp. by Bouteaux (2005) at Ngebung. Comparison of her measurements with a larger dataset was considered usefull to potentially narrow down these identifications. (What species do the Ngebung *Axis* -deer belong to?)
Cervus kendengensis	*Rusa* ?	Included	Included	This species is similar in size and morphology to modern *Cervus (Rusa) timorensis* (Dubois 1908). (Is *C. kendengensis* synonymous with *C.timorensis* or any of the other larger species from the Pleistocene of Java?)
Cervus zwaani	*Rusa* ? *Axis* ? *Hyelaphus* ?	Included	not included	According to Zaim (2003) *Cervus zwaani* is indistinguishable from *Axis lydekkeri*. Contrary to Von Koenigswald (1933), Zaim (2003) also states that there are no size differences between this species and *A. Lydekkeri*. (Is *Cervus zwaani* a synonim for *Axis lydekkeri* ?)
Cervus stehlini	*Rusa* ?	Included	not included	Von Koenigswald (1933) recognized Cervus stehlini as a separate species, albeit very similar in size and morphology to *Cervus (Rusa) timorensis*. (Is this species related to- or perhaps even synonymous with- *Cervus (Rusa) timorensis* ?)
Cervus timorensis/ Cervus hippelaphus (Pleistocene Java)	*Rusa*	Included	not included	Certain specimens were identified by von Koenigswald (1933, 1934) as *Cervus hippelaphus*, a junior synonym of Cervus *timorensis*, the extant Javan Rusa (Bouteaux 2005)
Cervus sp. (Pleistocene Sumatra)	*Rusa*	Included	Included	These fossils of the (sub-)genus *Rusa* have never been identified to species. Given the generally modern nature of the rest of the fauna (De Vos 1983) and the modern distribution of *Rusa*, it is likely they belong to *Cervus (Rusa) unicolor*. (To what fossil and/or modern deer species are the remains of *Cervus* sp. most closely related?)
Cervus unicolor (Pleistocene Laos, Vietnam)	*Rusa*	Included	not included	Measurements of this species from the Southeast Asian mainland were included by means of comparison.

Table 4

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Modern Species	Subgenus	Number of specimens used in linear morphometric analysis	Number of specimens used in geometric morphometric analysis
Chital (*Axis axis*)	*Axis*	68	14
Bawean deer (*Axis kuhlii*)	*Hyelaphus*	2	2
Hog deer (*Axis porcinus*)	*Hyelaphus*	23	8
Red deer (*Cervus elaphus*)	*Cervus*	not included	14
Sambar (*Cervus unicolor*)	*Rusa*	13	11
Javan rusa (*Cervus timorensis*)	*Rusa*	15	8
Philippine spotted deer (*Cervus alfredi*)	*Rusa*	4	3
Philippine deer (*Cervus mariannus*)	*Rusa*	2	2
Eld's deer (*Cervus eldii*)	*Rucervus*	not included	5
Barasingha (*Cervus duvaucelii*)	*Rucervus*	not included	4
Père David's deer (*Elaphurus davidianus*)	*Elaphurus*	not included	5
Fallow deer (*Dama dama*)	*Dama*	not included	5
Fossil Species/specimens	**Subgenus**	**Number of specimens used in linear morphometric analysis**	**Number of specimens used in geometric morphometric analysis**
Axis lydekkeri	*Hyelaphus* ?	140	3
Axis javanicus	*Hyelaphus* ? *Axis* ?	3	not included
Axis sp. (Ngebung)	*Hyelaphus* ? *Axis* ?	5	not included
Cervus kendengensis	*Rusa* ?	28	15
Cervus zwaani	*Rusa* ? *Axis* ? *Hyelaphus* ?	7	not included
Cervus stehlini	*Rusa* ?	4	not included
Cervus timorensis (Pleistocene Java)	*Rusa*	10	not included
Cervus sp. (Pleistocene Sumatra)	*Rusa*	115	10
Cervus unicolor (Pleistocene Laos, Vietnam)	*Rusa*	59	not included

Table 5

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	C. kendengensis	*A. kuhlii*	*A. axis*	*A. porcinus*	*C. mariannus*	*C. alfredi*	*A. lydekkeri*	*A.* sp. (Ngebung)	*A. javanicus*	*C. stehlini*	*C. swaani*	*C. hippelaphus* (fossil)	*C. timorensis*	*C.* sp. (Sumatra)	*C.unicolor* (fossils mainland)	*C.unicolor*
C. kendengensis	_	**<0.001**	**<0.001**	**<0.001**	**0.044**	**0.006**	**<0.001**	**<0.001**	0.079	**0.002**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. kuhlii	**<0.001**	_	**0.007**	0.354	0.694	0.427	0.467	0.721	0.106	0.091	0.310	**<0.001**	**0.005**	**<0.001**	**<0.001**	**<0.001**
A. axis	**<0.001**	**0.007**	_	**<0.001**	0.362	0.263	**<0.001**	**0.005**	0.100	**0.003**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. porcinus	**<0.001**	0.354	**<0.001**	_	0.871	0.749	**0.010**	0.794	**0.002**	**<0.001**	**0.042**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C. mariannus	**0.044**	0.694	0.362	0.871	_	0.938	0.505	0.751	0.255	0.163	0.309	**0.003**	**0.044**	**<0.001**	**<0.001**	**<0.001**
C. alfredi	**0.006**	0.427	0.263	0.749	0.938	_	0.110	0.629	0.153	0.077	0.269	**<0.001**	**0.019**	**<0.001**	**<0.001**	**<0.001**
A. lydekkeri	**<0.001**	0.467	**<0.001**	**0.010**	0.505	0.110	_	0.365	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
A. sp. (Ngebung)	**<0.001**	0.721	**0.005**	0.794	0.751	0.629	0.365	_	**0.039**	**0.024**	0.274	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**
A. javanicus	0.079	0.106	0.100	**0.002**	0.255	0.153	**<0.001**	**<0.001**	_	0.538	**0.043**	**0.044**	0.687	**<0.001**	**<0.001**	**0.002**
C. stehlini	**0.002**	0.091	**0.003**	**<0.001**	0.163	0.077	**<0.001**	**0.024**	0.538	_	**0.045**	0.080	0.685	**<0.001**	**<0.001**	**<0.001**
C. swaani	**<0.001**	0.310	**<0.001**	**0.042**	0.309	0.269	**<0.001**	0.274	**0.043**	**0.045**	_	**<0.001**	**0.005**	**<0.001**	**<0.001**	**<0.001**
C. hippelaphus (fossil)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**	**<0.001**	**0.044**	0.080	**<0.001**	_	**<0.001**	**<0.001**	**<0.001**	**0.003**
C. timorensis	**<0.001**	**0.005**	**<0.001**	**<0.001**	**0.044**	**0.019**	**<0.001**	**0.001**	0.687	0.685	**0.005**	**<0.001**	_	**<0.001**	**<0.001**	**<0.001**
C. sp. (Sumatra)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	_	**<0.001**	**<0.001**
C. unicolor (fossils mainland)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	_	**<0.001**
C. unicolor	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**	**<0.001**	_

Table 6

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PC	Eigenvalue	% variance
1	0.00324146	60.064
2	0.0011354	21.039
3	0.000372339	6.8994
4	0.000286388	5.3068
5	0.000114931	2.1297
6	7.97E-05	1.4762
7	4.16E-05	0.77122
8	3.70E-05	0.68564
9	2.56E-05	0.47496
10	1.79E-05	0.33124
11	1.58E-05	0.29325
12	7.54E-06	0.13977
13	6.76E-06	0.12519
14	5.24E-06	0.097036
15	4.25E-06	0.078699
16	2.16E-06	0.039945
17	8,03E-07	0.014875
18	7.54E-07	0.013971
19	6.09E-07	0.011283
20	1.85E-07	0.0034326
21	9.67E-08	0.0017928
22	6.93E-08	0.0012844
23	5.89E-08	0.001091
24	4.86E-10	9.01E-06
25	3.47E-10	6.43E-06
26	1.09E-10	2.02E-06

Table 7

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	A. axis	*A. kuhlii*	*A. lydekkeri*	*C. elaphus*	*C. kendengensis*	*D. dama*	*C. duvaucelii*	*E. davidianus*	*C. eldi*	*A. porcinus*	*C. alfredi*	*C. timorensis*	*C. unicolor*	*C. mariannus*	*C. sp. (Sumatra)*
A. axis	_	**0.0095**	**0.0013**	**0.0001**	**0.0001**	**0.0003**	**0.0031**	**0.0001**	**0.0005**	**0.0001**	**0.0133**	**0.0001**	**0.0001**	**0.0083**	**0.0001**
A. kuhlii	**0.0095**	_	0.4902	**0.0082**	**0.0071**	**0.0467**	0.0725	**0.0490**	**0.0462**	0.3848	0.0983	**0.0430**	**0.0094**	0.3338	**0.0157**
A. lydekkeri	**0.0013**	0.4902	_	**0.0008**	**0.0013**	**0.0189**	**0.0273**	**0.0364**	**0.0167**	0.3334	0.0963	**0.0123**	**0.0018**	0.2061	**0.0032**
C. elaphus	**0.0001**	**0.0082**	**0.0008**	_	**0.0001**	**0.0003**	**0.0029**	**0.0001**	**0.0284**	**0.0001**	**0.0038**	**0.0001**	**0.0005**	**0.0253**	**0.0001**
C. kendengensis	**0.0001**	**0.0071**	**0.0013**	**0.0001**	_	**0.0001**	**0.0006**	**0.0004**	**0.0002**	**0.0001**	**0.0015**	0.2524	**0.0001**	0.1580	0.0545
D. dama	**0.0003**	**0.0467**	**0.0189**	**0.0003**	**0.0001**	_	**0.0080**	**0.0083**	**0.0081**	**0.0007**	**0.0174**	**0.0007**	**0.0003**	**0.0478**	**0.0004**
C. duvaucelii	**0.0031**	0.0725	**0.0273**	**0.0029**	**0.0006**	**0.0080**	_	**0.0080**	**0.0172**	**0.0024**	**0.0276**	**0.0074**	**0.0060**	0.0664	**0.0140**
E. davidianus	**0.0001**	**0.0490**	**0.0364**	**0.0001**	**0.0004**	**0.0083**	**0.0080**	_	**0.0078**	**0.0010**	**0.0172**	**0.0036**	**0.0204**	**0.0493**	**0.0004**
C. eldi	**0.0005**	**0.0462**	**0.0167**	**0.0284**	**0.0002**	**0.0081**	**0.0172**	**0.0078**	_	**0.0011**	**0.0190**	**0.0010**	**0.0024**	**0.0497**	**0.0019**
A. porcinus	**0.0001**	0.3848	0.3334	**0.0001**	**0.0001**	**0.0007**	**0.0024**	**0.0010**	**0.0011**	_	**0.0066**	**0.0009**	**0.0001**	0.1294	**0.0005**
C. alfredi	**0.0133**	0.0983	0.0963	**0.0038**	**0.0015**	**0.0174**	**0.0276**	**0.0172**	**0.0190**	**0.0066**	_	**0.0056**	**0.0044**	0.1006	**0.0038**
C. timorensis	**0.0001**	**0.0430**	**0.0123**	**0.0001**	0.2524	**0.0007**	**0.0074**	**0.0036**	**0.0010**	**0.0009**	**0.0056**	_	**0.0082**	0.6736	0.5149
C. unicolor	**0.0001**	**0.0094**	**0.0018**	**0.0005**	**0.0001**	**0.0003**	**0.0060**	**0.0204**	**0.0024**	**0.0001**	**0.0044**	**0.0082**	_	0.4959	**0.0019**
C. mariannus	**0.0083**	0.3338	0.2061	**0.0253**	0.1580	**0.0478**	0.0664	**0.0493**	**0.0497**	0.1294	0.1006	0.6736	0.4959	_	0.3152
C. sp. (Sumatra)	**0.0001**	**0.0157**	**0.0032**	**0.0001**	0.0545	**0.0004**	**0.0140**	**0.0004**	**0.0019**	**0.0005**	**0.0038**	0.5149	**0.0019**	0.3152	_

Table 8
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	C. kendengensis	*C. alfredi*	*C. timorensis*	*C. unicolor*	*C. mariannus*	*C*. sp.	Total
C. kendengensis	7 (46.6 %)	0	2 (13.3 %)	1 (6.6 %)	1 (6.6 %)	4 (26.6)	15
C. alfredi	0	2 (66.6 %)	0	1 (33.3 %)	0	0	3
C. timorensis	2 (25 %)	0	4 (50 %)	0	0	2 (25 %)	8
C. unicolor	2 (16.6 %)	1 (8.3 %)	0	8 (66.6 %)	1 (8.3 %)	0	12
C. mariannus	0	0	0	1 (50 %)	0	1 (50 %)	2
C. sp.	4 (40 %)	0	2 (20 %)	0	2 (20 %)	2 (20 %)	10
Total	15 (30 %)	3 (6 %)	8 (16 %)	11 (22 %)	4 (8 %)	9 (18 %)	50

	C. Kendengensis/ timorensis/ sp.	*C. alfredi*	*C. unicolor*	*C. mariannus*	Total
C. Kendengensis/ timorensis/ sp.	29 (87.8 %)	0	1 (3 %)	3 (9 %)	33
C. alfredi	0	2 (66.6 %)	1 (33.3 %)	0	3
C. unicolor	2 (16.6 %)	1 (8.3 %)	8 (66.6 %)	1 (8.3 %)	12
C. mariannus	1 (50 %)	0	1 (50 %)	0	2
Total	32 (64%)	3 (6 %)	11 (22 %)	4 (8 %)	50

Figure 1
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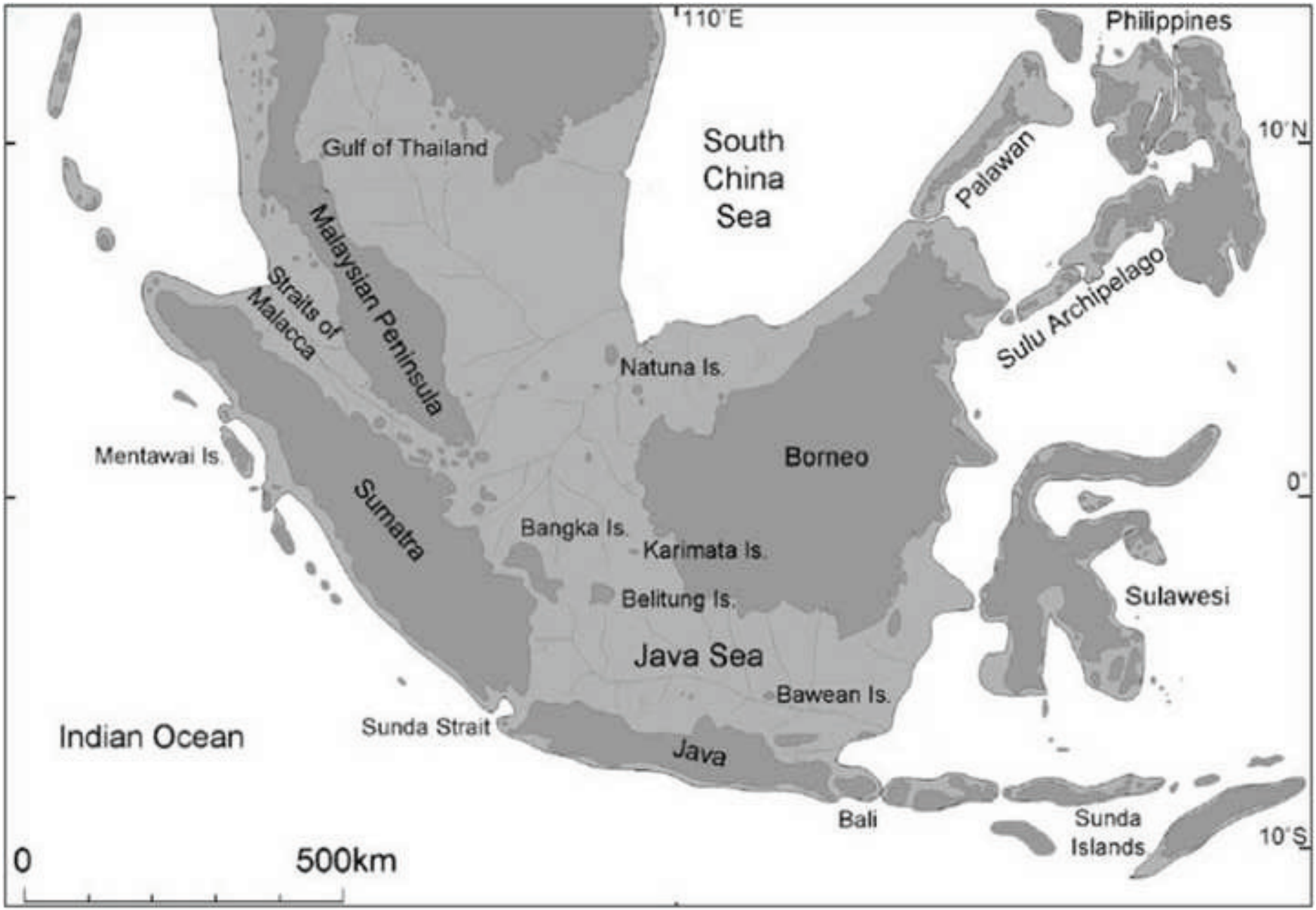

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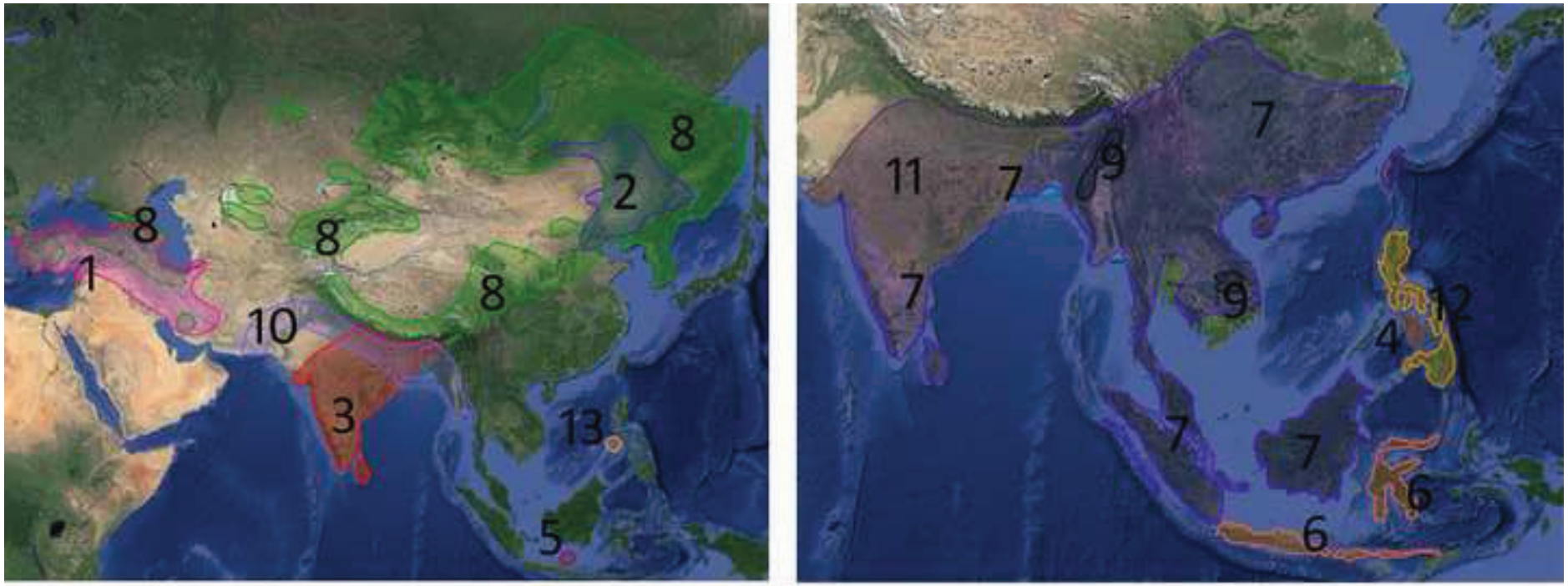

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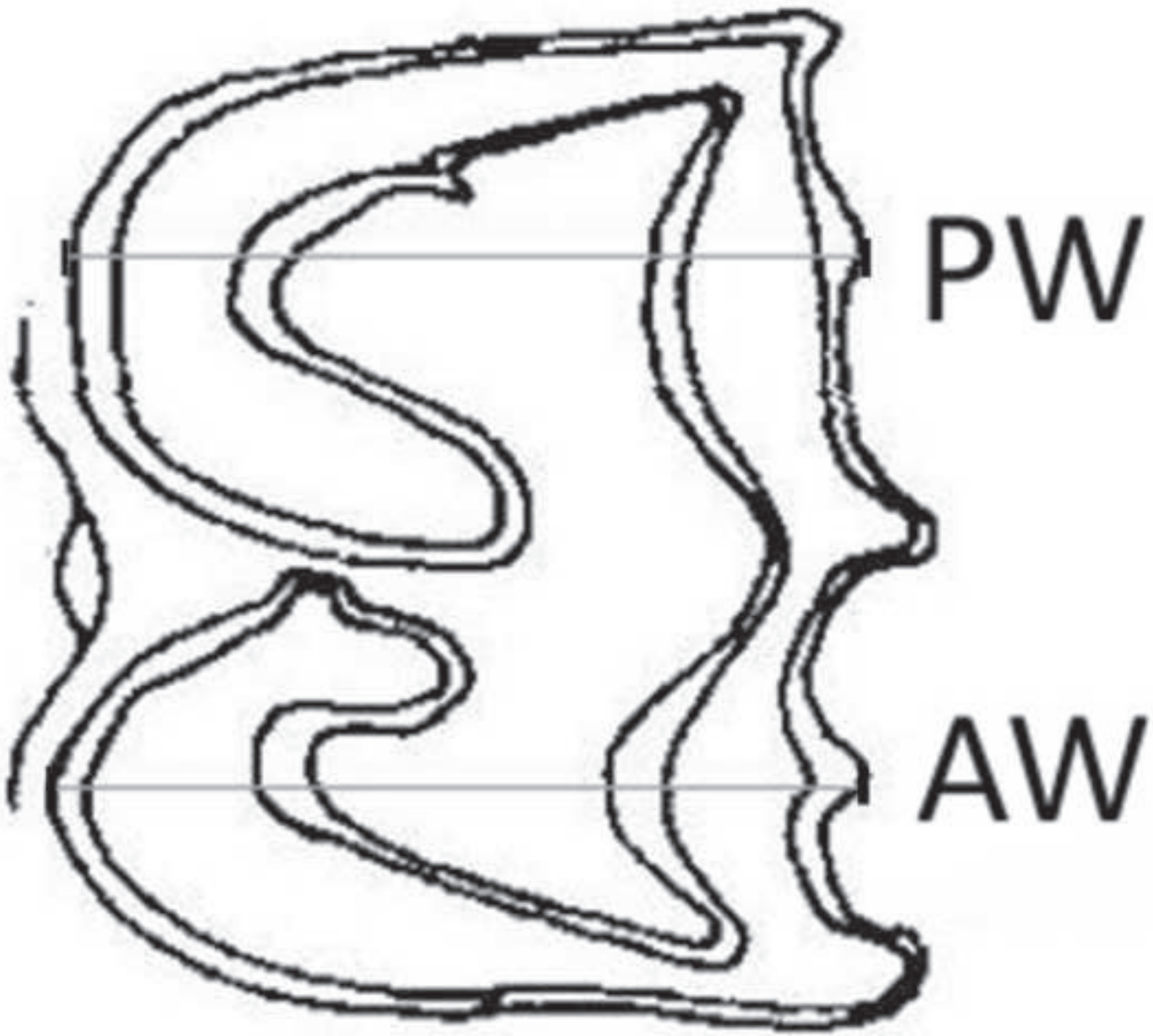

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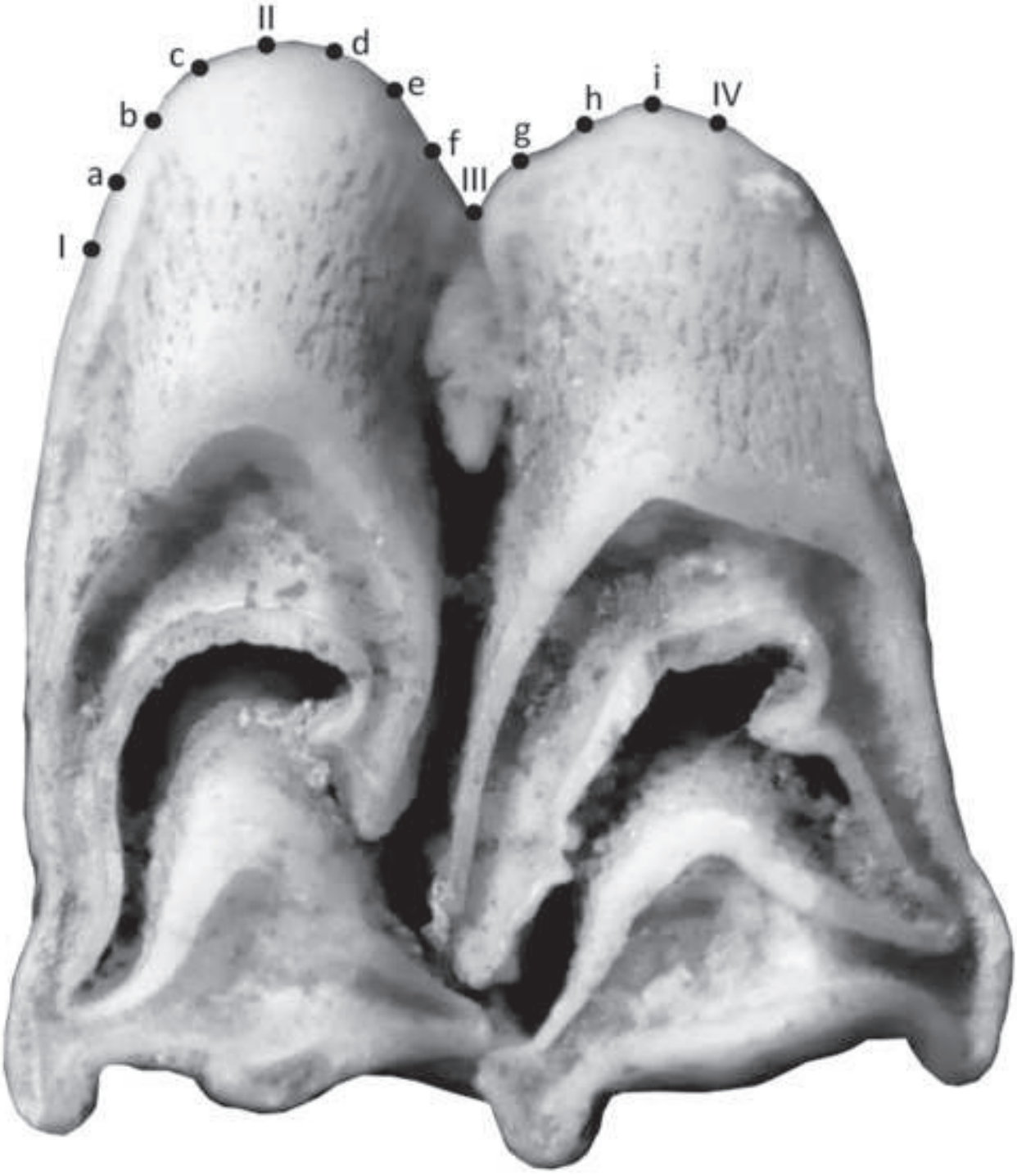

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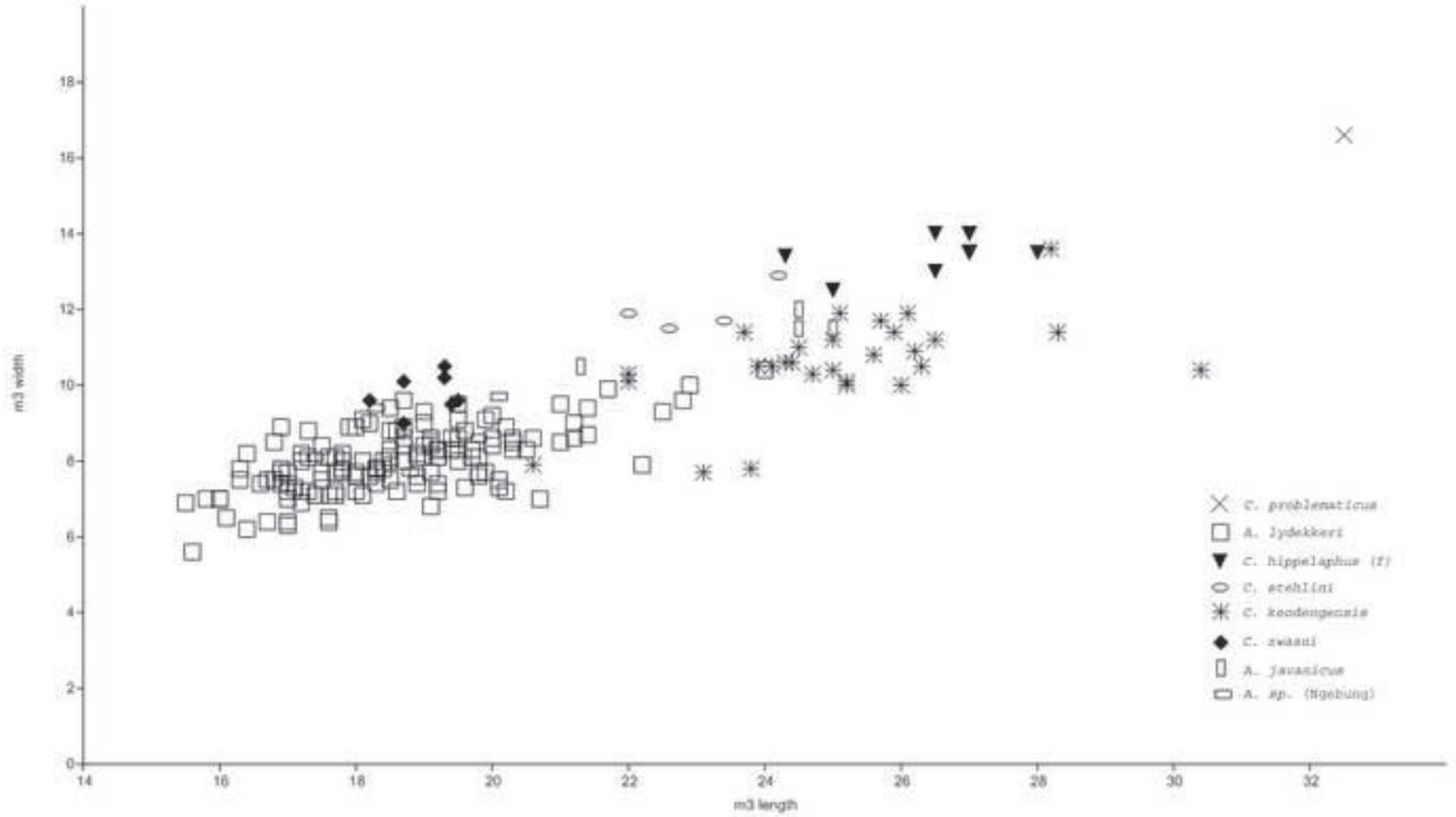

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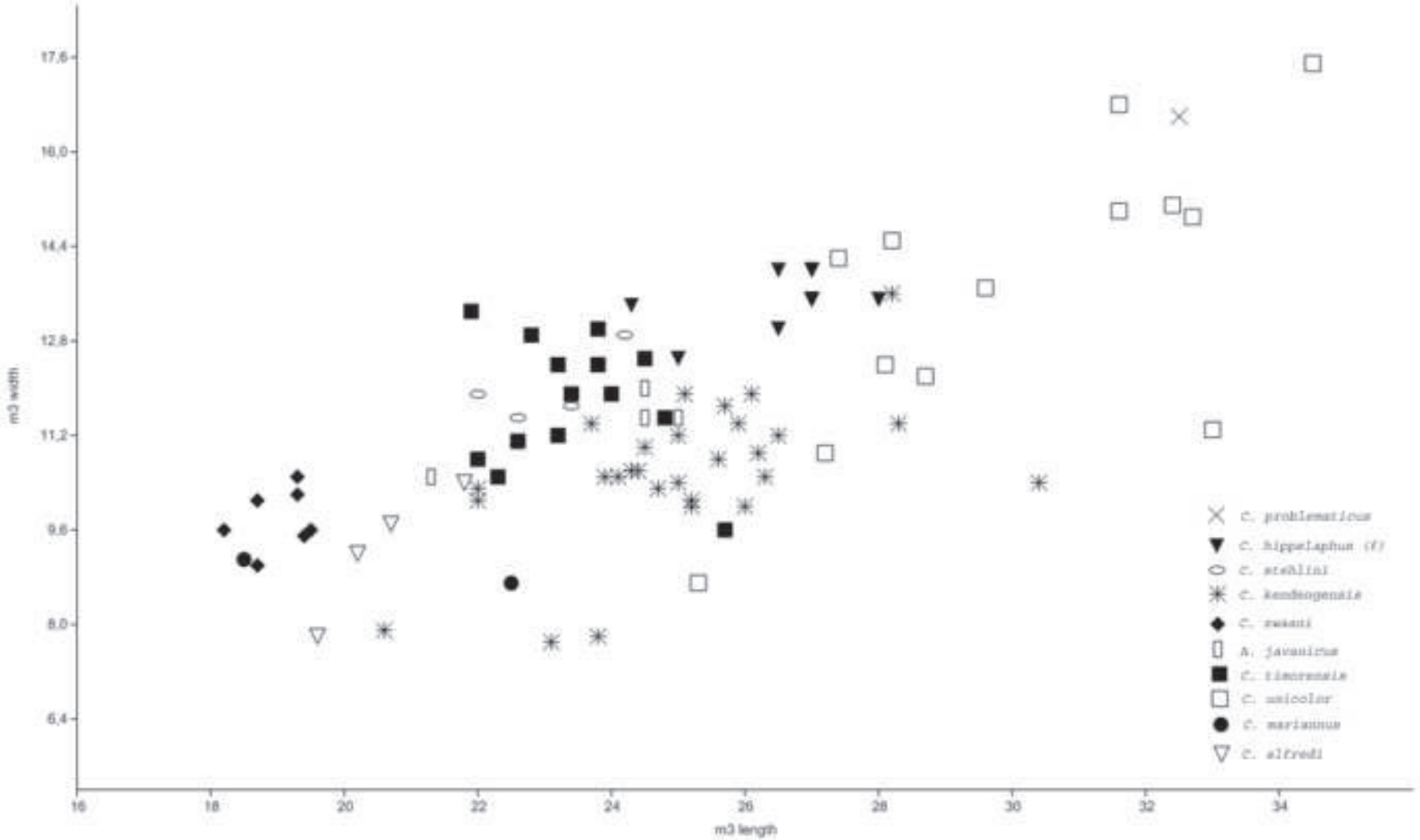

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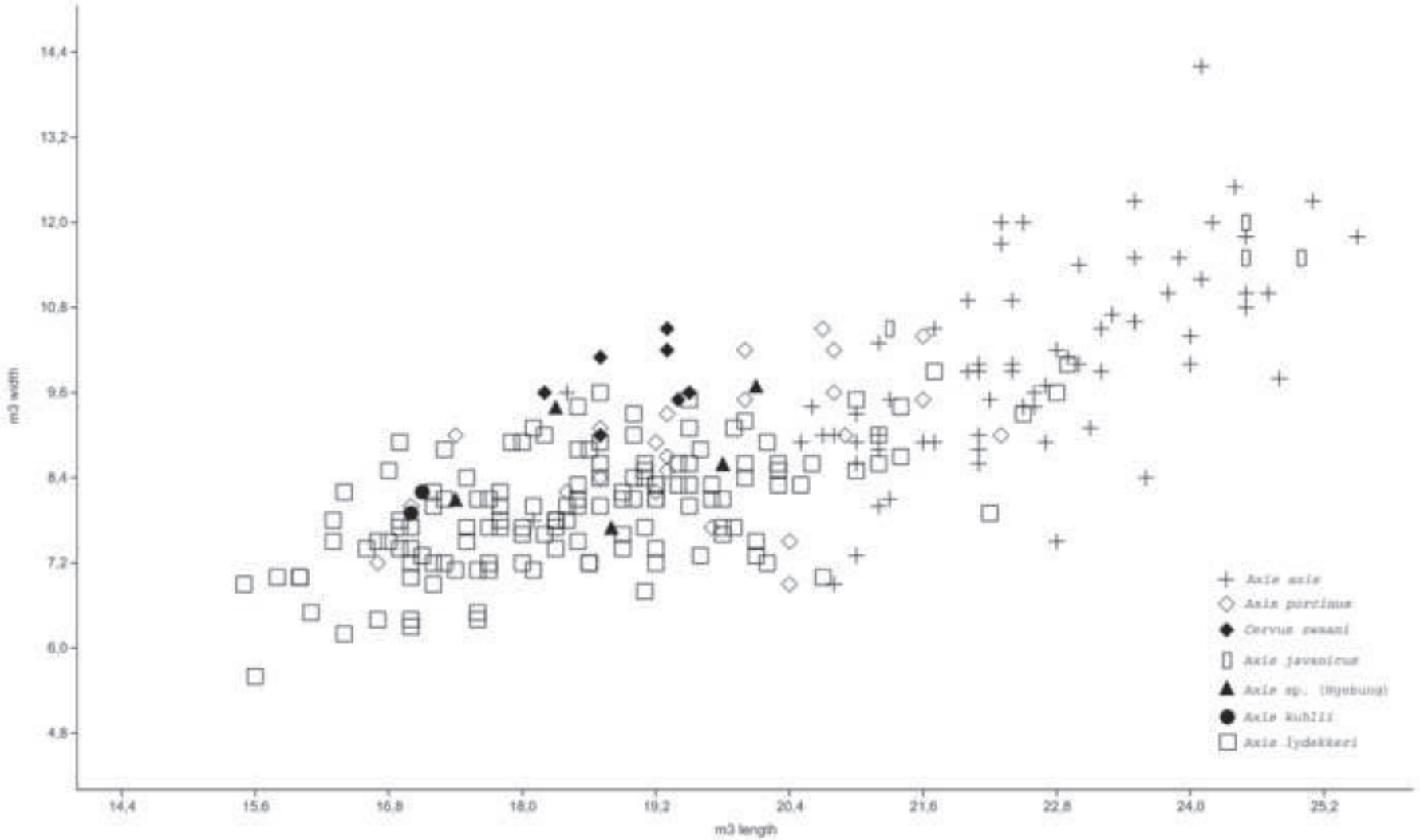

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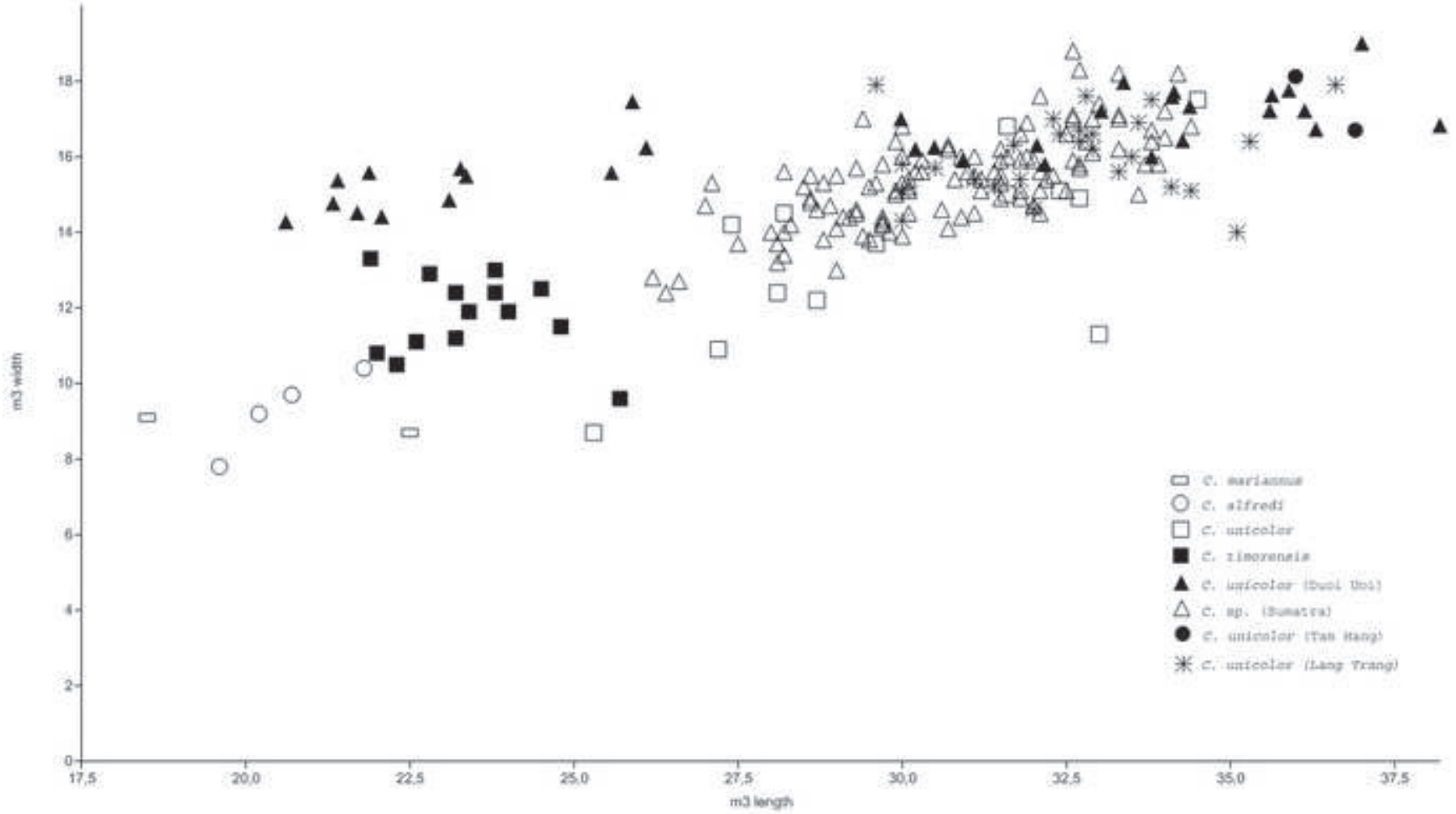

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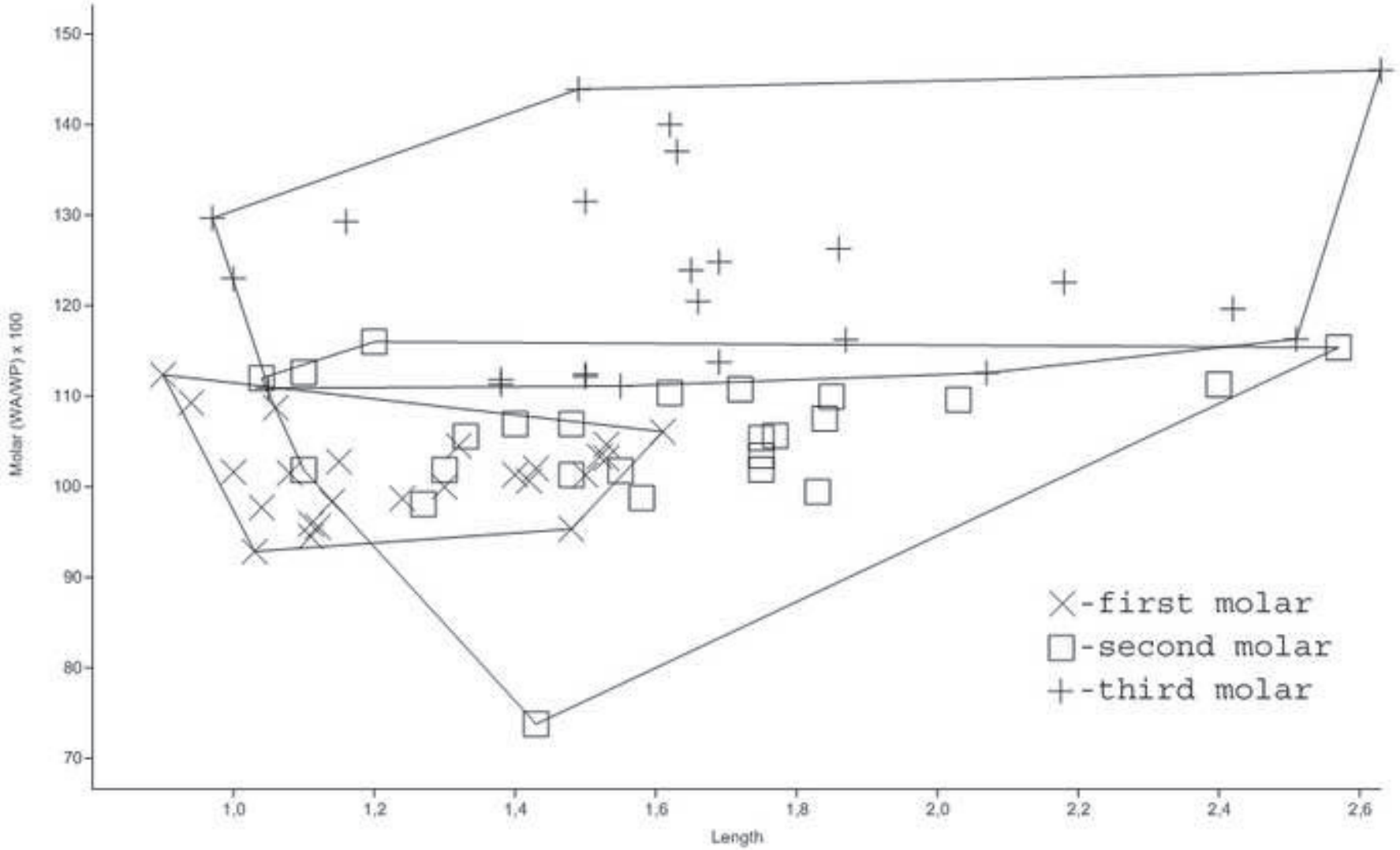

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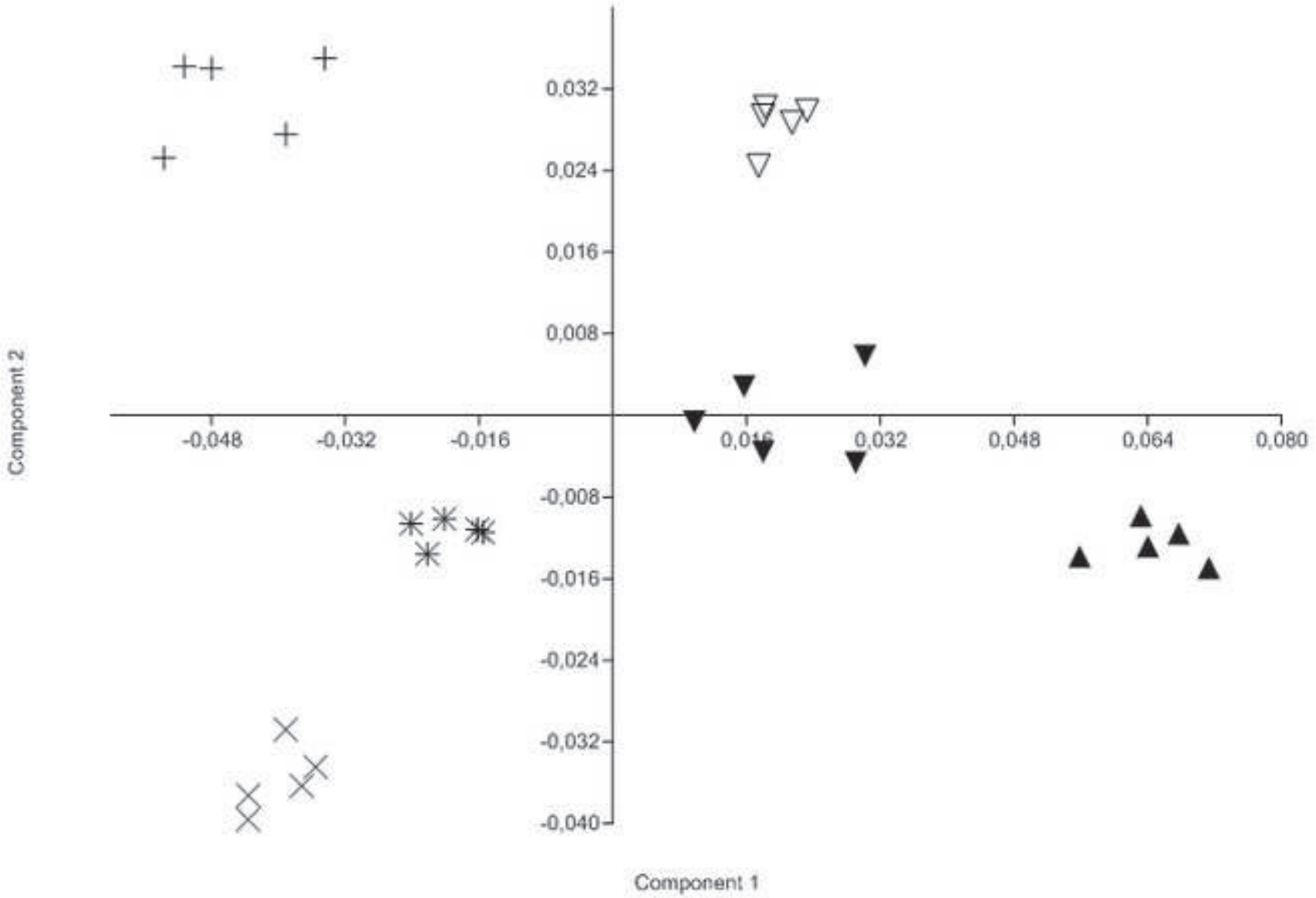

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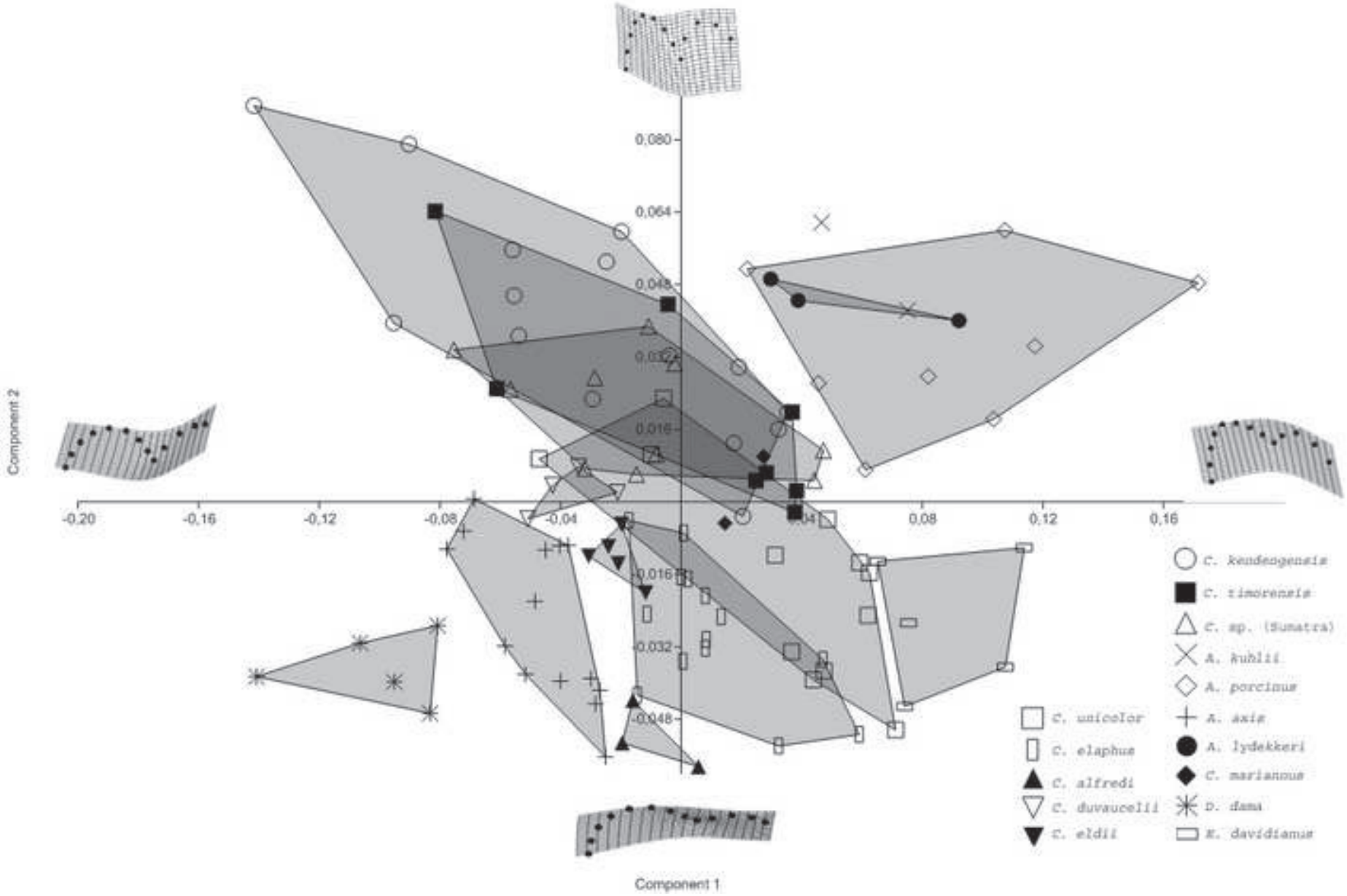

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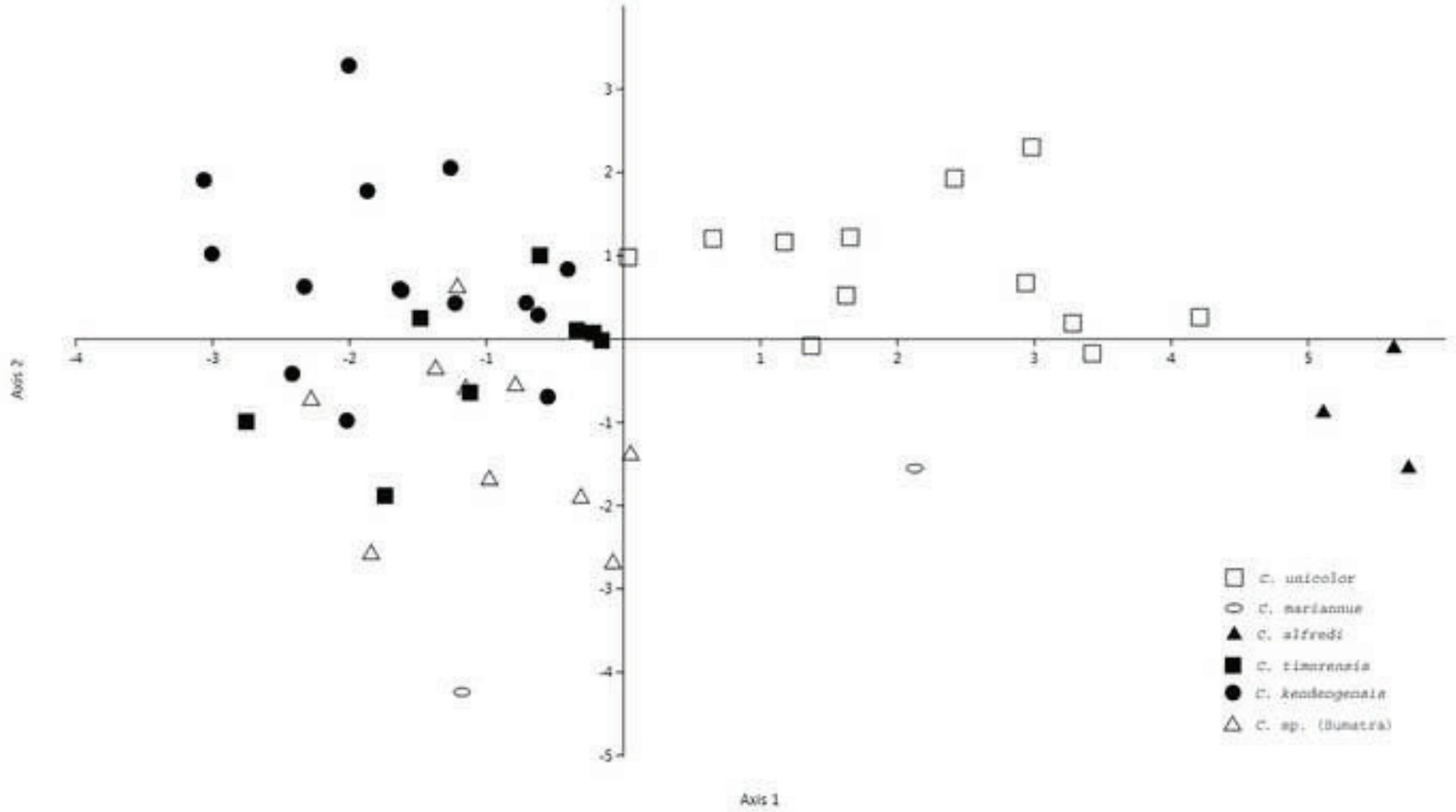

Appendix A

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Appendix B

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